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COMITÉ DE RÉDACTION

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LA QUESTION DE LA SENSIBILITÉ DES ABEILLES A L'ULTRA-VIOLET

Par E. HEINTZ

(Laboratoire de Psychologie animale, Faculté des Sciences, Strasbourg.)

Depuis les travaux de v. Frisch et de A. Kuhn sur la vision des Abeilles, on sait que ces animaux sont sensibles à un large domaine de longueurs d'onde s'étendant depuis 310 m μ jusqu'à 650 m μ environ.

En employant des méthodes quantitatives, Bertholf a trouvé un maximum de sensibilité dans le visible situé vers 550 m μ . Dans l'ultra-violet, il trouve un maximum très élevé, à 365 m μ , que Sander n'a pas retrouvé. Ce maximum est environ cinq fois plus fort que le maximum à 550 m μ .

Si ce maximum existe réellement, on peut se demander si la grande sensibilité de l'Abeille dans l'ultra-violet provient uniquement de l'œil ou si un sens dermatoptique entre en jeu, comme le fait pressentir Bertholf. Le présent travail a été entrepris pour répondre à ces questions.

Nous avons employé une méthode de phototropisme avec des Abeilles non dressées en ne présentant aux Abeilles, à chaque fois, qu'une couleur spectrale d'intensité donnée et en déterminant le nombre de réactions attractives pendant un temps donné à l'avance.

DISPOSITIF

Sur la paroi C (fig. 1) en plexiglas dépoli (12 \times 12 cm) d'une boîte à lumière A d'une longueur de 50 cm, on projette en E, à l'aide d'un miroir concave M et d'une lentille L₂, l'image agrandie de la fente d'un monochromateur. L'image ainsi formée a 12 cm de hauteur et 2 mm de largeur. La fente d'entrée du monochromateur Kipp et Zonen avec prisme en quartz et optique à miroirs est éclairée par l'intermédiaire de la lentille en quartz L₁ soit par une lampe à vapeur de mercure H. P. 80, soit par une lampe à filament incandescent rectiligne placées en S.

Un monochromateur simple comme celui que nous avons employé fournit des lumières monochromatiques contenant un petit pourcentage de lumière diffuse de toutes longueurs d'onde. Pour supprimer cette lumière parasite, nous avons pris soin de placer sur le trajet lumineux,

- (1) K. v. FRISCHE. — *Zool. Jahrb. Abt. Allg. Zool. u. Physiol. Tiere*, 1914, 35, 1-182.
- (2) A. KUHN et R. POHL. — *Naturwissenschaften*, 1921.
- (3) A. KUHN. — *Ztschr. vergl. Physiol.*, 1927, 5, 762-800.
- (4) L. M. BERTHOLF. — *J. agricult. Res. Wash.*, 1931, 42, 379-419.
- (5) L. M. BERTHOLF. — *J. agricult. Res. Wash.*, 1941, 43, 703-713.
- (6) W. SANDER. — *Ztschr. f. vergl. Physiol.*, 1934, 20, 267-286.

devant la fente d'entrée du spectrographe, différents filtres ; des filtres Schott transparents à l'ultra-violet et opaques pour le visible pour purifier l'ultra-violet, et des filtres interférentiels pour le visible.

Le spectrographe et le dispositif d'éclairage ont été enfermés dans des boîtes étanches à la lumière, de sorte qu'aucune lumière parasite ne pouvait pénétrer dans la boîte à lumière A.

La boîte A destinée à recevoir les Abeilles est revêtue à l'intérieur de carton noir ; son couvercle supérieur est en verre à travers lequel on observe les Abeilles.

Pour permettre l'observation en pleine obscurité, on éclaire la paroi

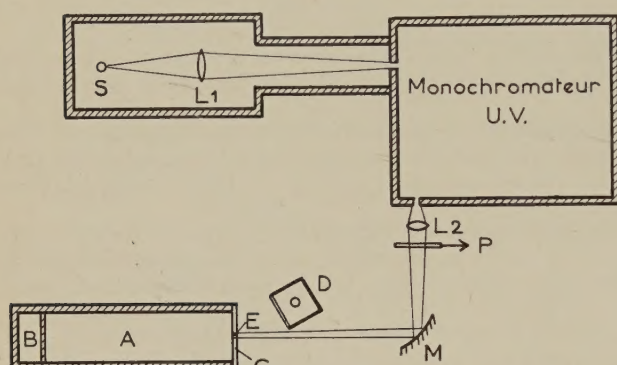


FIG. 1. — Dispositif expérimental pour la mesure de la sensibilité des Abeilles aux différentes couleurs spectrales.

A, boîte à lumière ; C, écran en plexiglas dépoli ; L_1 , L_2 , lentilles en quartz ; M, miroir ; P, cellule photo-électrique formant en même temps obturateur ; monochromateur UV ; S, source de lumière ; D, éclairage auxiliaire rouge.

dépolie C avec une lumière auxiliaire rouge D de longueur d'onde supérieure à $650 \text{ m}\mu$ à laquelle les Abeilles ne sont plus sensibles.

Lorsque la paroi C n'est pas éclairée, sauf par ladite lumière rouge, les Abeilles se meuvent sur le fond de la boîte et sur les parois, au hasard. Le couvercle de verre est toujours moins fréquenté, l'adhérence pour les Abeilles étant moins bonne que sur le carton.

En démasquant à l'aide d'un obturateur P la lumière, les Abeilles se mettent à grimper très exactement le long de l'image E de la fente avec une fréquence qui dépend de la longueur d'onde employée et de l'intensité de l'éclairement. En général, les Abeilles montent le long de l'image de la fente, les descentes étant beaucoup moins fréquentes. Arrivées vers le haut de l'image, elles se dirigent soit à gauche, soit à droite et se meuvent ensuite au hasard le long des parois latérales. Lorsqu'elles atteignent le fond de la boîte, elles perçoivent à nouveau la lumière et marchent, à partir de ce moment, en ligne droite vers l'image lumineuse. Ainsi il se forme un va-et-vient continu avec des passages successifs sur l'image de la fente.

Nous avons pris comme test de sensibilité le nombre de montées ou de descentes (nombre de visites) le long de l'image de la fente pendant un temps donné, qui était de trois minutes dans nos expériences.

De temps à autre, il arrive qu'une Abeille ne parcourt pas toute la longueur de l'image. Nous ne comptons comme réactions positives que les Abeilles parcourant au moins les trois quarts de la longueur totale de l'image.

Le but de la première partie du présent travail consiste à déterminer le nombre de visites de l'image de la fente en fonction de l'énergie lumineuse employée, et ceci pour un certain nombre de longueurs d'ondes.

Nous avons essayé d'abord de mesurer directement les différentes énergies employées à l'aide d'une pile thermo-électrique Kipp reliée à un galvanomètre sensible et étalonnée auparavant en valeurs absolues (ergs/cm^2) avec une lampe Hefner. Mais, comme les énergies faibles ne donnaient plus de mesures suffisamment précises, nous avons remplacé la pile thermo-électrique par une cellule photo-électrique étalonnée à l'aide de la pile. Elle est placée en P sur une glissière et nous servait en même temps d'obturateur de la lumière. Les diverses intensités lumineuses employées ont été obtenues en faisant varier à l'aide de rhéostats le régime de la lampe S.

Pour chaque intensité lumineuse employée, on a placé dix Abeilles nourries et adaptées pendant une demi-heure à l'obscurité dans la boîte à lumière A, puis on a déterminé le nombre de montées ou de descentes le long de l'image de la fente pendant trois minutes. Nous avons répété cette expérience dix fois, mais à chaque fois avec dix autres Abeilles n'ayant pas encore servi. Ainsi, chaque point représentatif sur les courbes obtenues représente la moyenne de 10 mesures indépendantes avec chaque fois dix Abeilles.

RÉSULTATS

En opérant comme nous venons de le dire, nous avons trouvé que le nombre des réactions est proportionnel au logarithme de l'énergie lumineuse employée, et ceci dans le domaine des longueurs d'onde employées depuis $300 \text{ m}\mu$ jusqu'à $665 \text{ m}\mu$ (cf. Loi de Weber-Fechner).

Sur la figure 2 sont représentées un certain nombre de ces droites logarithmiques. Pour les faibles énergies, elles s'incurvent légèrement pour tendre rapidement vers zéro. En prolongeant ces droites jusqu'à leur intersection avec l'axe des abscisses, on obtient des énergies limites que nous avons prises comme seuil de la sensibilité. Ces seuils coïncident sensiblement avec les énergies non significatives observées.

Pour les fortes énergies, les droites s'incurvent également. Elles deviennent toutes horizontales pour un même nombre de visites égal à environ 60. A ce moment, les Abeilles se déplacent dans la boîte à lumière avec la vitesse de marche maximum possible. Elles ont tendance à voler à partir de ce degré d'excitation.

Sur les droites de la figure 2 nous avons indiqué par un trait vertical la grandeur de l'erreur type sur la moyenne. Les résultats obtenus sur les parties droites des courbes sont très significatifs. Le test « t » de Student Fisher est en général plus grand que 7 et atteint 25 dans quelques cas.

La pente des droites ainsi obtenues représente la sensibilité de l'Abeille dans le domaine spectral étudié. En traçant la courbe de ces pentes en

fonction des longueurs d'onde, on obtient une courbe à deux maxima, l'un dans le visible, vers $550 \text{ m}\mu$, et l'autre plus élevé dans l'ultra-violet, vers $365 \text{ m}\mu$ (fig. 3).

L'allure de cette courbe ressemble en gros à la courbe obtenue par Bertholf ; elle confirme les valeurs des longueurs d'onde des maxima trouvés par cet auteur et confirme aussi les limites de la sensibilité spectrale des Abeilles : 300 et $650 \text{ m}\mu$ environ.

D'après les données de la figure 2, on peut tracer maintenant des courbes

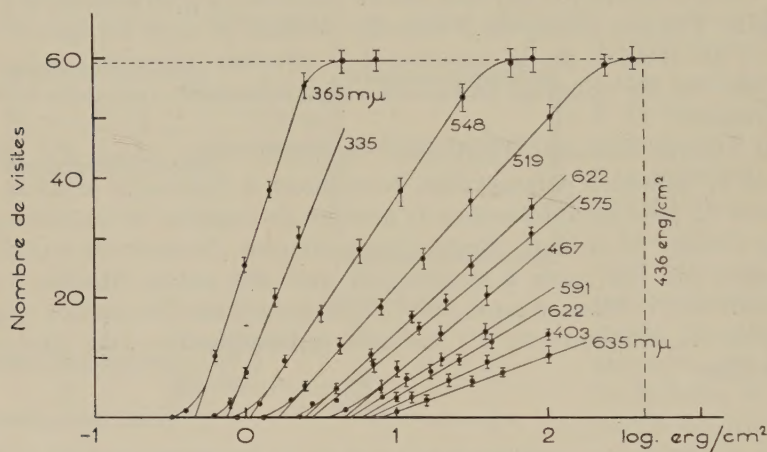


FIG. 2. — Sensibilité des Abeilles à différentes couleurs spectrales en fonction de l'énergie lumineuse.
En ordonnées : sensibilité = nombre de visites. En abscisses : énergie en $\log \text{ ergs/cm}^2$.

à égales énergies. La figure 4 présente une de ces courbes pour une énergie de 5 ergs/cm^2 . Nous avons reporté sur cette courbe, en pointillé, la courbe à énergie stimulatrice relative donnée par Bertholf, en faisant coïncider les ordonnées des deux courbes pour $\lambda = 550 \text{ m}\mu$. Les deux courbes sont très voisines ; elles ne diffèrent que dans l'ultra-violet. Remarquons qu'en comparant la courbe de Bertholf avec les nôtres le meilleur accord est obtenu pour des énergies de l'ordre de 5 ergs/cm^2 .

Nous pensons que le désaccord sur les ordonnées dans l'ultra-violet pour les deux courbes est dû au fait que Bertholf dans ses expériences ne partait pas de lumières d'égale énergie. Il a comparé le nombre de visites obtenues en lumières monochromatiques avec le nombre de celles obtenues dans une lumière blanche d'une intensité fixe, et il déterminait les énergies relatives de lumière blanche nécessaires pour obtenir le même nombre de visites qu'avec les lumières spectrales. Il divisait les valeurs ainsi obtenues par les valeurs relatives de l'énergie des diverses lumières spectrales employées. Déjà Sander qui n'avait pas trouvé de maximum à $365 \text{ m}\mu$, dans sa critique du travail de Bertholf, remarque que ce calcul n'était justifié que si, pour les différentes longueurs d'onde, la valeur de l'excitation dépend de la même façon de l'énergie, ce qui n'est pas le cas. Les pentes

variables de nos droites (fig. 2) confirment également cette critique, mais montrent qu'un maximum élevé à $365\text{ m}\mu$ existe néanmoins. Si nous avons trouvé des résultats conformes à ceux de Bertholf, ce n'est qu'en

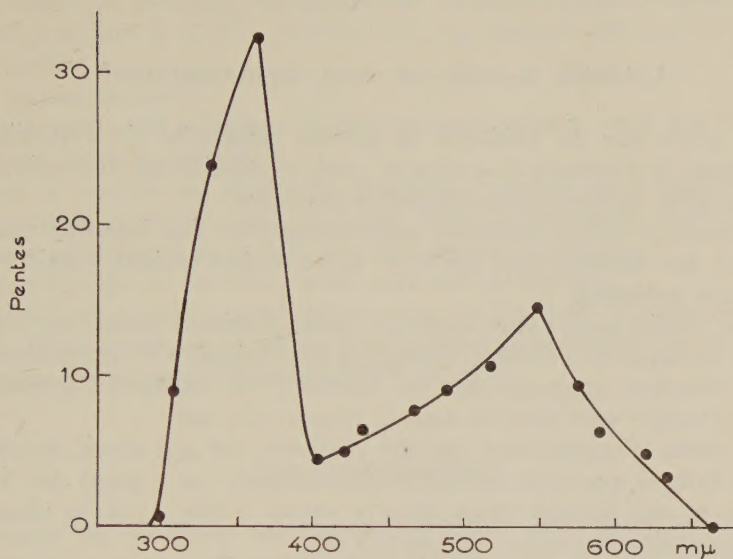


FIG. 3. — Courbe de sensibilité de l'Abeille en fonction de la longueur d'onde.
En ordonnées : pentes des droites de la figure 2. En abscisses : longueurs d'onde en $\text{m}\mu$.

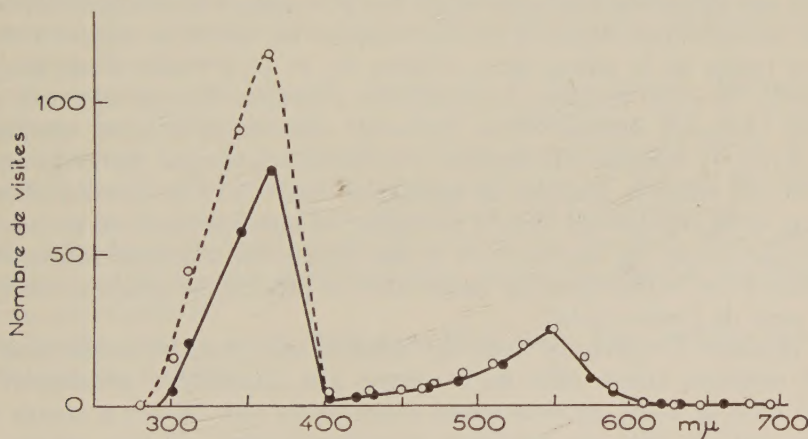


FIG. 4. — Courbe de sensibilité de l'Abeille en fonction de la longueur d'onde.
—●—●— Courbe à énergie égale, 5 ergs/cm².
—○—○— Courbe à énergie stimulatrice relative d'après Bertholf (5).

employant des énergies faibles. La discordance eût été plus forte avec des énergies fortes.

Sander, voulant opérer avec la même énergie pour les différentes longueurs d'onde, a malheureusement employé des énergies trop fortes (436 ergs/cm^2) et, de ce fait, il n'a pu trouver de maximum à $365\text{ m}\mu$, attendu

qu'avec de telles énergies il a obtenu pour beaucoup de longueurs d'onde (en particulier 365 et 550 m μ) le maximum de visites possible (voir notre fig. 2, dans la partie horizontale des courbes logarithmiques).

L'Abeille a-t-elle un sens dermatoptique?

Après avoir mis en évidence la grande sensibilité de l'Abeille dans l'ultra-violet, il s'agissait de savoir si cette sensibilité est due uniquement aux yeux ou si un sens extra-rétinien y participe.

Pour trancher cette question, nous avons fait des mesures comparatives avec des Abeilles dont les yeux et les ocelles étaient vernis, et avec des Abeilles normales.

Comme vernis, nous avons employé, après plusieurs essais, un vernis au collodion à l'éther et à l'alcool, chargé de noir animal. Ce vernis bien adhérent est très bien supporté par les Abeilles. Des vernis à l'acétone et à l'acétate d'amyle sont mortels dans la plupart des cas.

Deux sortes d'expériences ont été réalisées. On a d'abord employé la même technique que celle décrite précédemment. On a placé des Abeilles aux yeux et aux ocelles vernis dans la partie A (fig. 1) de la chambre à lumière en opérant avec $\lambda = 365$ et 548 m μ .

Les Abeilles se meuvent au hasard dans la boîte, mais aucune ne suivait le tracé de l'image de la fente sur le plexiglas dépoli C.

Dans une deuxième expérience nous avons remplacé le plexiglas dépoli C par un plexiglas non dépoli et l'avons illuminé sur toute sa surface avec la lumière totale de la lampe ultra-violette H. P. 80 à l'aide d'une lentille en quartz. De cette manière, toute la boîte à lumière A était traversée par un flux lumineux intense. On a introduit alors dans le petit compartiment B (fig. 1), étanche à la lumière, des Abeilles normales. Après quelques minutes, on retire la planche de séparation entre A et B. Les Abeilles se dirigent alors rapidement vers le plexiglas, où elles essayent de se rapprocher de la source. En moyenne 80 % des Abeilles se trouvent ainsi continuellement sur le plexiglas. Le même effet se produit en irradiant uniquement avec de l'ultra-violet.

En répétant l'expérience avec des Abeilles aux yeux et ocelles noircis, on ne constate aucun effet de ce genre. Les Abeilles se promènent au hasard dans la boîte, qu'elles soient éclairées ou non ; il n'y a aucun rassemblement du côté du plexiglas, ni augmentation de leur vitesse de locomotion.

Nous concluons, d'après ces deux expériences, à la non-existence d'un sens dermatoptique chez l'Abeille. Toute leur sensibilité aux excitations lumineuses est due aux yeux.

RÉSUMÉ ET CONCLUSIONS

On a étudié la réaction (attraction) de l'Abeille à des lumières monochromatiques dans le spectre depuis 300 m μ jusqu'à 665 m μ et d'intensités variables.

Nous avons montré :

1^o Qu'il existe des relations logarithmiques entre le taux des réactions et l'énergie spectrale employée ;

2^o Que la courbe de sensibilité spectrale possède deux maxima, l'un dans le visible, vers 550 m μ , et l'autre dans l'ultra-violet, vers 365 m μ . Ce dernier est environ deux fois plus intense que le premier ;

3^o Que l'Abeille ne possède pas de sens dermatoptique.

Nos résultats confirment en partie ceux de Bertholf, et complètent ces derniers. Finalement, nous avons montré pourquoi Sander n'a pu mettre en évidence le maximum de sensibilité à 365 m μ .

Zusammenfassung.

Es wurde die Reaktion von Bienen auf monochromatische Lichter und variabler Intensität im Spektrum von 300 bis 665 m μ untersucht. Das Spaltbild eines Spektrographen wurde auf die Wand einer Versuchskammer vergrößert abgebildet. Als Test der Reaktion wurde die Zahl der Bienen genommen die während einer vorgegebenen Zeit auf das Spaltbild zugehen und ihm entlanglaufen.

Dabei ergaben sich folgende Resultate : 1) Eine lineare Abhängigkeit zwischen der Reaktionszahl und dem Logarithmus der verwendeten Spektralenergie für alle verwendeten monochromatischen Lichter. 2) Eine spektrale Empfindlichkeitskurve mit zwei Maxima bei 550 und bei 365 m μ . Das Letztere ist etwa doppelt so intensiv wie das im Sichtbaren.

Die gefundenen Resultate bestätigen z. Teil die Resultate Bertholf's und ergänzen sie. Es konnte gezeigt werden, warum bei Sander das Max. bei 365 m μ nicht auftritt.

Weiterhin konnte nachgewiesen werden, dass *Apis mellifica* keinerlei Lichthautsinn besitzt.

OBSERVATIONS ON THE NESTS OF INITIAL COLONIES OF *NEOTERMES TECTONAE* DAMM. IN TEAK TREES*

by L. G. E. KALSHOVEN

(*Blaricum, Netherlands.*)

One of the first discoveries of importance concerning the biology of *Neotermes tectonae* Damm. living in teak trunks, was that new colonies are apparently started in dead branches in the crowns of the trees. This was found by me during incidental observations made as early as 1924 near Tjepu in Central Java, before the systematic study of the bionomics of the termite was put on the programme of forest-entomological investigations at the Institute for Plant Diseases in Bogor in 1925 (Kalshoven, 1924). Since then, many observations have confirmed the statement. Originally it was thought that the *Neotermes* alates could only enter the wood through old boreholes and similar places (Kalshoven, 1930). Experiments conducted in 1935-1936 proved however that they have no need of such holes to gain entrance into the wood—although they readily use them if present—but that they are able to gnaw their way right into soft parts of rotten wood and there make their first hole. The experiments also showed that the swarming alates are directly attracted to pieces of rotten wood, even when these are not attached to a tree (Kalshoven, 1957). The meeting of partners, the formation of the first small cavity or nuptial chamber and its seclusion from the outside were already described in some details in my thesis (1930).

Extensive observations on the occurrence of initial *Neotermes* colonies in dead parts of the crowns of teak trees, carried out in 1935-1938 to gather data on the time of the first infestation of new teak plantations and the increase of the population in subsequent years (Kalshoven, 1959.), have provided various additional notes on the habits of the termite in establishing itself in dead limbs, and afterwards moving from them into sound wood.

During these investigations it was found that very young colonies and even newly settled pairs of dealates can be discovered if dead branches collected from the tree crowns are carefully examined and the bark peeled off. A few pellets or small clusters of yellow clayey excrements sticking to the outside will betray the presence of the termites.

Starting points of new colonies.

DEAD BRANCHES. — Every teak tree of some age growing in the uniform, closely-planted plantations has several dead branches in its crown, their death being mainly caused through lack of light for the older branches in the lowest level, and particularly so during the period of strong growth in height of the trees, which are competing with each other in the upper canopy of the stands.

* The preparation of this paper has been made possible thanks to a grant received from the Netherlands Organization for the Advancement of Pure Research (Z. W. O.).

According to numerous counts made during the examination of several plots the number of dead branches per tree proved to be:

4 on the average in			5-year old teak plantations.		
5	—		6	—	—
5 or 6	—		7	—	—
7 or 8	—		8	—	—
12	—		10	—	—
16	—		12	—	—

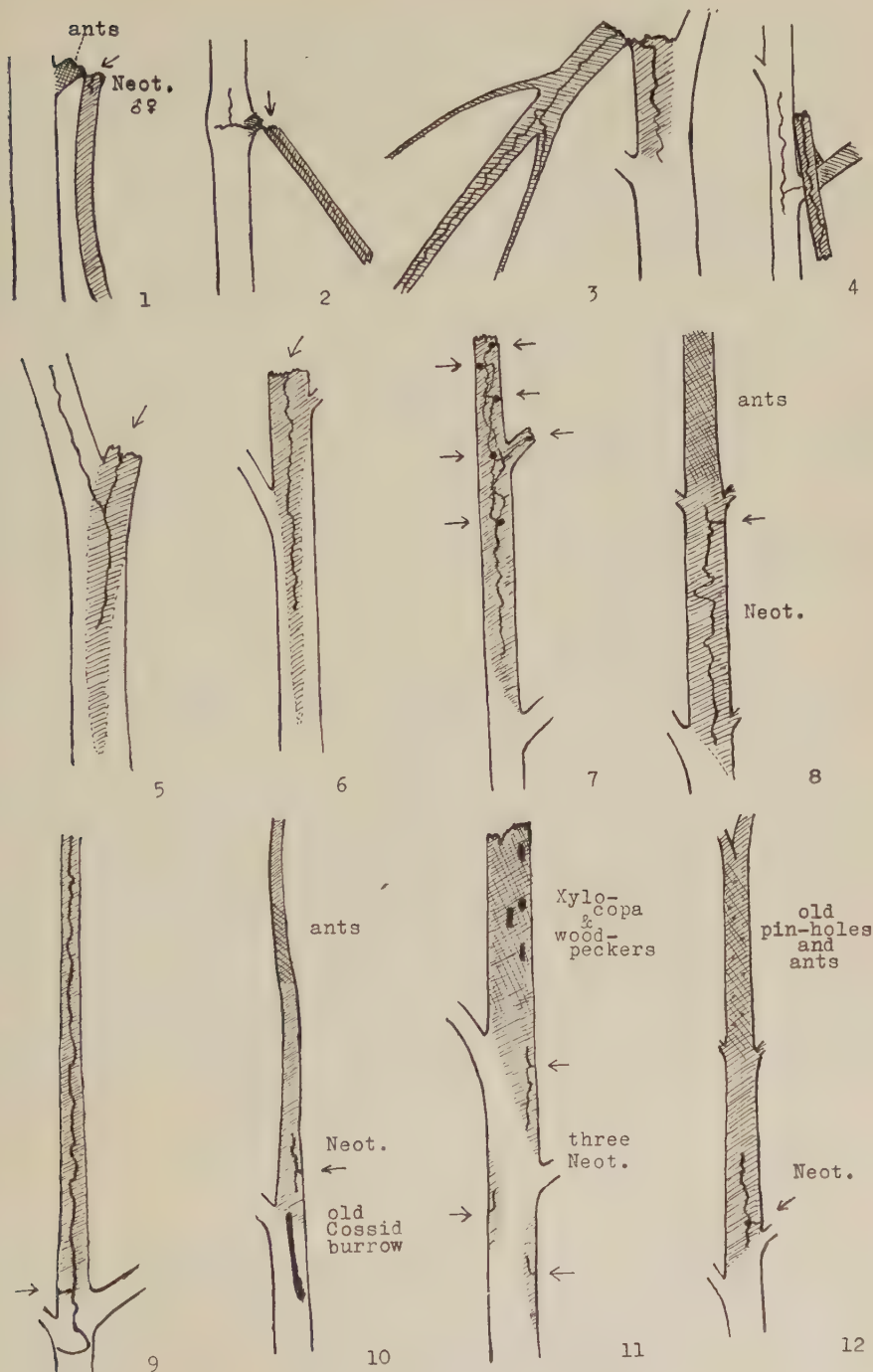
During these extensive investigations about 0.1-1.3 % of these dead branches were found to be inhabited by *Neotermes* (Kalshoven, 1959.). Most of them were primary branches, a much smaller part secondary ones—that is side branches of still living main branches—of which there are not many present on the teak trees in young cultivations.

In an ecological respect dry primary and secondary branches will have the same value for the starting of *Neotermes* colonies as also have the dead tops (see later paragraph).

These dead limbs are up to 2 or 3 m in length and have a diameter of 1.5-3.5 cm—sometimes even 5 or 6 cm—at the base. The dwindling of the branches and their ensuing death appear to be a rather rapid process, but afterwards the dead parts remain attached to the trees for a long time. During this period the thin, less ligneous tops will break off, the bark will loosen and be shed, and the wood will gradually become entirely rotten.

TEXT OF PLATE

PLATE. — Sketches of particular situations of incipient or young nests of *Neotermes tectonae* in the dead parts—shaded in the drawings—in the crowns of living teak trees. The arrows point to the original entrance into the wood. The extent of the nest is marked by a single winding gallery. Double shading indicates parts inhabited by ants. — *Fig. 1.* Long broken branch hanging down, a pair of dealates has settled near the point of fracture, an ant colony inhabits the snag on the trunk. — *Fig. 2.* Remaining part of a broken branch, inhabited by a circa 2-year old colony which has already extended its galleries, via the snag, into the living wood; there the trunk shows an initial swelling. — *Fig. 3.* Large broken dead top, harbouring a large population of *Neotermes* divided over the stump and the hanging part and found to include 7 young colonies, see p. 240 sub (e). — *Fig. 4.* *Neotermes*-infested fallen part of a dead top, which has become hooked in the axil of a dead branch; the thriving colony, 2 or 3 years old, is moving from the loose broken piece into the living trunk. — *Fig. 5.* Nest in part of trunk with a rotten heart, the latter resulting from rain-water penetrating into the fracture, where a former top has broken off; the galleries of the circa two year old colony extend into the wood of the sound, new top. — *Fig. 6.* The same, a circa one year old colony is still living entirely in the tissues of the decayed heart. — *Fig. 7.* Dead top, riddled by intertwining galleries of some 6 young colonies, see p. 239 sub (d). — *Fig. 8.* Dead stunted top, its upper half inhabited by a large ant colony, just below it the nest of *Neotermes* colony, circa one year old. — *Fig. 9.* Lengthy dead top, its basal part harbouring a young colony, which has made a circular gallery under the bark of the lower living part. — *Fig. 10.* Old burrow of the Cossid *Xyleutes ceramica*, just below a dead top and possibly one of the causes of the dying back, an ant colony inhabiting a portion of the dry terminal part and a 4 month old *Neotermes* colony in its base. — *Fig. 11.* Stunted dead top with *Xylocopa* holes and traces of woodpeckers in the terminal part and three incipient nests of *Neotermes*, only 4 months old, in necrotic patches at a lower level. — *Fig. 12.* Dead top, a large upper section showing old pin-holes of ambrosia beetles and inhabited by ants, a small *Neotermes* colony, one year old, is established in the base.



This process may take some years. During this time the basal part becomes sunk into the trunk as a result of the increase in girth of the tree.

POINTS OF ENTRANCE INTO DEAD LIMBS. — Not infrequently the dying branches are inhabited by Cerambycids, less often by some species of ambrosia beetles (*Xyleborus* spp.) and, as decomposition of the wood progresses, by larvae of Tenebrionids and similar saprophagous species. Sometimes the large holes of carpenter bees (*Xylocopa* spp.) are found in large dead limbs (p. 233, fig. 11).

Observations that a colony founding pair of *Neotermes* had actually used the exit holes of a Cerambycid beetle are comparatively few in number and these holes appeared to originate mainly from *Xylotrechus buqueti* C. et G., a species which commonly occurs in dying poles and limbs of teak. (At least 5 other species of small and medium-sized Cerambycids have been reared from dead limbs of teak on different occasions.) No definite proof was obtained that the *Neotermes* dealates had used the "pinholes" of ambrosia beetles. In most cases where a young colony had started its borings somewhere in the middle of a branch no traces of preceding secondary borers were found and the dealates must have gained entrance through an opening in the dead bark or must have eaten their way into the rotten tissue.

The number of cases in which young colonies had been started in the terminal part of a dead branch were comparatively large and in all these instances the original top had broken off, giving the dealates the opportunity to find an easy entrance into the exposed soft pith at the point of fracture. Even in dead branches, which still had a length of 2 or 3 m, incipient colonies were found in the top-part. The starting of the colonies somewhere in the middle of a branch appeared to be decreasing in frequency in proportion to the remaining part of the limb being shorter. Yet side-entrances have been found in basal parts of broken branches as short as 25 cm. The use of the actual base of a dead branch near the trunk for entering has been observed to be rare.

Four exceptional cases were found where pairs of *Neotermes* dealates had settled in branches, 1.5-2 cm in diameter, which had broken near the base but still had remained attached to the stump on the trunk with some fibres (p. 233, fig. 1). Here the dealates had every time entered at the point of fracture in the pith of the hanging dead part. Only a few eggs were present with them, but observations have made it probable that young colonies can further develop under these circumstances and even may reach the main trunk (p. 233, fig. 2).

DEAD TREE TOPS. — In some forest compartments examined a considerable percentage of the trees had dead tops, apparently mainly caused by the suppression of backward individuals by the more or less dominant neighbouring trees. Bad soil conditions and periods of extreme drought may also have contributed to the frequency of dead tops in the young

plantations. In rare cases the top-limb had been weakened or killed by the large Cossid borer *Xyleutes ceramica* Walk., the bee-hole borer (p. 233, fig. 10). The dead tops gradually break down and deteriorate as do the dead branches, but their basal parts remain for as long as 4-6 years, as indicated by the number of annual growth rings of the suckers which had replaced them. During this time they appear to be rather attractive for swarming alates in search of places to alight and settle. Thereby the relatively broad places of fracture apparently offer the most suitable places for entrance (p. 233, fig. 5 and 6). Besides, they can enter sideways or in the base—and this not so rarely (p. 233, fig. 9-12)—in a similar manner as in dead branches.

SNAGS. — Points of entrance of great importance appear to be the snags which remain after the dead branches have broken off near the base. These snags may be only a few cm in length, but it may take several years before they are grown over by new wood and bark layers of the trunk. Notwithstanding their small dimensions they appear to be readily detected by the swarming *Neotermes* alates.

It is somewhat surprising that only very rarely are these snags starting points for inner rot of the trunk and where this is the case they appear to have rather more than less attraction for the swarming alates.

BLIGHTS AND WOUNDS. — During the most intensive phase in the search for initial infection of the teak plantations by *Neotermes* a few cases were found where the crown or a large branch showed rotten places and incipient colonies were found living in the wood just at these points. The diseased parts appeared to be caused in part by the attack of the bark-destroying *Corticium salmonicolor* fungus, which may thrive in the humid atmosphere of dense plantations. In another instance the wounds were caused by the cracking of the bark through the bending of the upper-trunk in a gale. This kind of damage, whereby the wood becomes exposed, occurs not infrequently in too slender trees.

There is also a note in my files about *Neotermes*-infestation in the lower part of the trunk where it had been too deeply cut by an adze in marking the tree.

As may be clear all such wounds are only very incidental starting points for new colonies of *Neotermes*.

Direction of the first galleries.

As a general rule the galleries of new colonies—consisting of some 10 larvae acting as workers and one small soldier besides the parent couple—are excavated in the direction of the grain of the wood. In thin branches they often follow the pith and where old wood-dust packed tunnels of Cerambycid larvae are present they will follow these over some distance.

When a colony is founded in the top of a dead branch, the galleries are soon extended over some 10 cm and more in the direction of the base. Where colonies are started somewhere in the middle of a branch there is no strict rule about the direction the galleries are taking. Contrary to the expectation they are in many cases directed away from the trunk or upwards. In other instances, they run exclusively towards the base. The more general trend is for them to be made in both directions but in such a way that the downward part is much larger than the upward part. Where, finally, the colonies happen to have started at the very base of a dead limb, the first galleries are almost invariably directed away from the trunk.

Discussing now the apparent stimuli which regulate the direction taken by the young larvae in excavating their galleries, it is evident that the course of the grain of the wood is a main factor directing their tunnelling activities, and that there is no positive or negative geotaxis. However a second factor of importance may be a tendency to extend the galleries into those parts of the wood with the higher moisture content. This might explain the greater length of the downward part so often found in nests started in the middle of a branch, as this part by its greater thickness and its position may be less dry than the top-part. This may especially be the case during the pronounced dry season which lasts from April till October in the teak area of Central Java. As soon as the galleries are extended to the wood adjacent to the living tissues of the tree there will be sufficient access to moisture. It may be long, however, before the colonies reach this source.

It is not quite clear how the very young colonies can subsist in the thin top of lengthy dry branches during the long dry season when the wood must lose much of its moisture, while, moreover, the trees have shed their leaves and the bare crowns are fully exposed to the sun. In this connection it will be recalled that the *Neotermes* larvae can void their excrements either in the form of pellets—resembling those of the dry-wood termites, *Cryptotermes*—or in semi-liquid fashion, whereby cakes of clayey matter are accumulated. Probably the first form is mainly produced under relatively dry conditions and the second under moist conditions.

Expansion of the nest in dry limbs.

With the growth of the colony the galleries are extended and, in addition, cavities are eaten out in the wood. These excavations have often the form of chambers parallel to the circumference and are very narrow when measured radially. They are connected by narrow passages in the same way as has also been observed in the nests of *Cryptotermes* spp. Besides, many irregular cross galleries are also made. During these activities cylindrical layers of wood are spared and there remains a kind of skelet which supports the affected branches and tops for some time.

It has not been investigated whether the infested and hollowed parts break sooner than uninfested limbs, but it is striking that all colonies which were successfully extracted from the dead limbs appear to be complete with the parent couple present and without neoteinic individuals. This might hint at a rare occurrence of a breakage of the infested branch at the place where the colony houses.

In the extension of the longitudinal galleries the base of the branch will eventually be reached, and this all the sooner as the branch or stub is shorter and the colony has been started nearer the basal part. In this phase the galleries are extended exclusively in that portion of the branch which has become a part of the trunk and which has become sunk more deeply into the main body of the tree by the girth increment. The basal core or knob consists of dead wood, which, however, will have the same moisture content as the heart-wood of the tree.

This point in the expansion of the nest has very often been met with and it has become clear that the colonies will maintain this situation a long time before attacking the living tissues.

Prolonged subsistence on dry wood.

There have been numerous observations of well-developed *Neotermes* colonies composed of two or three score of individuals and therefore about 2-3 years old, which still had confined their activities to the wood of a large branch or a dry tree-top outside the main trunk. By far the most colonies of that size and age, however, have extended their galleries to the over-grown base or have already for some time penetrated the living trunk.

	COMPOSITION OF COLONY.				PART OF LIMB IN- HABITED.	EXTEN- SION OF NEST.	DIMENSIONS OF DEAD LIMB		MONTH OF COLL.
	♀♂	Eggs.	Larvæ and nymphs.	Sold.			Total length.	Diam. at base.	
a	♀♂	7	81 l.	3	top	144 cm	226 cm	4 cm	July
b	♀♂	3	112 l.	4	—	49 —	77 —	4 —	—
c	♀♂	11	118 l.	6	—	113 —	167 —	4 —	—
d	♀♂	6	156 l.	6	—	50 —	70 —	4 —	—
e	♀♂	7	191 l.	7	central	17 —	189 —	5 —	Aug.
f	♀♂	—	159 l. 175 n. VI 15 n. VII	5	whole branch	287 —	287 —	6 —	
g	♀♂		795 l. 77 n. VI	28	top	140 —	290 —	6 —	Aug.

The table above shows details of some extreme cases observed, in which the colonies had an even more prolonged life in the wood of dead limbs.

These seven examples show that *Neotermes* can build up fairly large colonies exclusively on the wood of dead branches without access to the living tissues of the main trunk. Items (f) and (g) clearly show that in rare cases the colonies can even reach full maturity—the stage in which the alates are formed—under these conditions. These colonies both contained nymphs with short wing pads (VI instar) and in item (f) also nymphs with long wing pads (VII instar). Especially in the latter case it was evident that the colony would release a number of alates in the next swarming season, about in the months of October to December.

It may be pointed out, however, that in all these exceptional cases the colonies were living in rather thick branches, viz. 4-6 cm in diameter, while most dry branches inhabited by young colonies measure only 1.5-3.5 cm at the base. Moreover in the cases (d) and (g) the field notes mention that the wood of the branches was only slightly decomposed. It must be admitted therefore that these colonies had possibly been started in a dry top of a branch which still had a green base at that time, and that the basal part had died off subsequently.

The move into the living parts of the trees.

Even where new colonies have been founded in snags of small dimensions they will very rarely extend their nests into any adjacent living tissues before the colony consists of from 30 to 60 individuals, thus being 1-1.5 years old. The small volume of dead wood available appears to be sufficient, which once more underlines the fact that these termites make a most economical use of their food.

When the colony eventually extends its activities to the green wood this is done in two ways: the galleries already present in the sunk base of the dead limb or snag are extended to the heart-wood of the main trunk, where they again follow the grain and therefore run vertically. This time most of the extension goes straight upwards, and only a much smaller part downwards. In the second place the termites start boring galleries and cavities into the sapwood immediately under the bark and this is done in the form of horizontal tunnels, encircling a part of the circumference (p. 233, fig 9), and of narrow chambers. Round holes are bored through the sound bark to the surface, apparently for the removal of excrements and for aeration.

In one peculiar instance, only once met with, a piece containing a *Neotermes* colony, fallen from a broken top, had been arrested in its fall by becoming hooked in the axil of a dead branch in the crown. Here the colony had succeeded in entering the wood of the living trunk via the base of the dead limb (p. 233, fig. 4).

In vigorous trees the damage done to the outer and cambial layers of

the wood includes a partial interruption of the sapflow and results in a formation of callus tissue and a broadening of the annual rings, causing a swollen part, first one sided, but gradually—as the activities of the colony continue—all around the place where the nest is located. The colony may already be living partially or wholly within the main trunk for some time before these swellings grow so large as to become conspicuous to the observer standing on the ground. As will be clear the process is quite the same where a colony enters from a dead secondary branch into a still living main branch, but—as mentioned before—this does not often occur in young cultivations.

Eventually the colony has moved entirely into the trunk or crown axis of the tree. The further formation of large cavities in the sapwood and chambers under the bark and the gradual shifting of the colony to higher parts in the trunk, where new swellings are formed, have been described in my first extensive paper on the bionomics of *Neotermes* (1930).

Coincidence of two or more initial colonies in the same dead part.

Several times it was found that more than one pair of dealates had settled or founded its colony quite near to each other in one and the same dead part in the tree crowns.

More commonly two or three pairs or incipient colonies were found inhabiting well separated nests at small distances—of 6-10 cm from each other—in dead branches and tree-tops. In some instances the galleries were excavated about at the same level making it impossible to extract the colonies separately.

Here are the details of a few cases in which even more pairs or young colonies were found sharing the same "micro-habitat".

(a) Four dealate pairs without brood found in the narrow space of a rotten snag of 6 cm length and 2.5 cm in diameter, the galleries penetrating downwards into the knob sunk into the tree trunk, 10.XII.1937. Apparently pairs very recently settled during the swarming season.

(b) Four similar pairs in a dead branch of 150 cm length, 4.5 cm in diameter, in short galleries, without brood.

(c) Three pairs of parents accompanied by 4, 6 and 8 larvae respectively in well separated galleries of 5-7 cm, and another three dealates with 8 larvae from apparently mixed galleries over a length of 9 cm, all having established themselves sideways in a dry branch without bark, 120 cm in length, 3 cm in diameter, the entrances being only 12-30 cm apart, 26.V. 1937. Evidently these incipient colonies had been started some 6 months previously.

(d) Eleven dealates, 6 eggs, 24 larvae and 5 small-sized soldiers extracted from intertwined galleries in a section, 36 cm long, of a dead tree-top of 120 cm length and 5 cm thick at the base, 25.V.1937. Most probably 5 (or 6) originally separate colonies, not older than half a year (p. 233, fig. 7).

(e) Thirteen dealates together with 142 larvae and 7 small sized soldiers collected from their galleries in a dead broken top, the top-part hanging down from the stub, total length 200 cm, diameter at the base 5 cm, 10.III.1937 (p. 233, fig. 3). Evidently, the populations of 7 initial colonies, which had got mixed during the collection, one of the parent specimens being lost.

(f) Fourteen dealates, out of which 5 pairs in well separated holes of 0.5-1 cm, in a dead tree top, 117 cm in length, 5 cm in diameter at the base, 7.XII.1937. Apparently, 7 very recently settled couples in the swarming season.

Considering that the total amount of material suitable for the establishment of *Neotermes* colonies and available in the teak plantations is very large, it may be thought surprising that several alates may happen to meet in definite parts of rather small dimensions dispersed over the numerous tree-crowns forming the vast canopy of the forests. However this observation may hint at comparatively large numbers of swarming sexuals and at a large measure of attractability of certain dead parts of the trees.

That the single dealates after alighting and finding a suitable place for entrance may soon be joined by a partner is a matter of attraction between the sexes, as has been shown in experiments in the laboratory and in the field (Kalshoven, 1930). Now it is a matter of speculation whether these neighbour colonies, being dependent on a restricted volume of wood, will keep separate for a long time or may sooner or later fuse into one. That the latter may occur has been observed in young colonies reared in small pieces of rotten wood and placed together in the laboratory. A fusion like this results in the elimination of one parent couple. On the other hand several cases of two pairs of parents found among large populations extracted from the same part of a trunk may be considered to be an indication that at least two colonies can continue living side by side without mixing, notwithstanding their galleries and cavities intertwine to a large extent.

Mortality in the initial period of the colonies.

In my treatise of 1930 particulars have been given about several kinds of predators preying on the swarming and alighting alates and on the newly settled pairs and their first brood during the time the nests are still rather superficially situated in the wood. Part of these data were gained in observations in artificial nests.

During the search for initial colonies in the tree crowns remarkable little evidence was obtained about agencies of a biotic or abiotic nature which threaten the colonizing alates and the young colonies with failure and extinction.

No indications were found, for instance, that newly settled pairs or

initial broods succumb through desiccation of the wood. On the other hand, it became still clearer that they could not suffer from excess of water. The galleries in the dead tops and branches are apparently built in such a manner that they are not drowned during heavy rain showers, at least not so long that losses to the colony might be caused. Moreover the colonies thrive in rotten or sound tissues which are soaked with water or have an abundance of sap (p. 233, fig. 5 and 6).

On four occasions dead pairs or single specimens of dealates were met with in their initial chamber or first gallery of 3-5 cm length. In one of these cases the couple had settled in diseased tissue affected by the *Corticium* fungus, but this could scarcely have caused their death as healthy colonies have also been found in *Corticium*-infested parts of the tree (see p. 235).

In another case out of 5 dealates found close together in the base of a dead branch one was dead, perhaps killed by a competitor.

In an incipient colony with 4 small larvae but still lacking, the small sized soldier one of the parents was dead.

In a few other cases initial galleries were found to be empty, again without any clue as to the cause.

During the examination of one plantation, seven cases came to hand where a first swelling in the trunk, measuring 6-16 cm in height, and clearly the work of *Neotermes*, did not show any inhabitants in the cavities. Similar cases were also found, but more rarely in other plots, and sometimes an ant colony had occupied the cavities. Though the conjecture appeared to be plausible that the ants might have killed the *Neotermes*-colony, there was no proof of it.

Finally it is worth mentioning that in the thousands of *Neotermes*-infested limbs and tops traces of a woodpecker were met with in one instance only and in this case they had opened the holes of carpenter bees and had left alone the termites (p. 233, fig. 11). This confirms the observation previously made (1930) that woodpeckers most surprisingly, practically do not feed on these termites, notwithstanding the fact that the latter are obtainable quite easily in the hollowed out and somewhat brittle dry branches. But perhaps the *Neotermes* are unpalatable to the birds.

Résumé.

Pendant l'essaimage, les imagos ailés de *Neotermes tectonae* sont attirés en grand nombre par les branches mortes ou les chicots des cimes des arbres de teck (*Tectona grandis*). Ces parties mortes, pour la plupart d'origine non pathologique, s'observent en abondance dans les plantations serrées, et elles restent attachées aux arbres longtemps, se décomposant peu à peu. Pour établir leur loge, les imagos attaquent très souvent la moelle exposée aux endroits où une partie terminale s'est détachée, ou bien ils transpercent latéralement les branches pourrissantes. Ils n'utilisent que rarement d'anciens forages abandonnés. Les colonies primaires sont sapro-

phages. Leurs galeries initiales suivent le fil du bois et sont tantôt dirigées vers le sommet, tantôt et le plus souvent vers la base des branches, ce qui s'explique peut-être par le plus fort degré hygrométrique des parties basales. Ordinairement, les galeries des colonies juvéniles s'étendent après un ou deux ans dans les parties vivantes de la cime ou du tronc, mais les colonies peuvent subsister pendant trois ans et plus sur le bois mort, atteignant exceptionnellement dans ce milieu la phase de première apparition des individus ailés. On peut trouver jusqu'à six colonies primaires dans la même branche. Bien qu'occupant la même partie limitée d'un arbre et possédant des galeries entremêlées, les colonies peuvent rester séparées très longtemps, du moins lorsque leur nombre n'excède pas deux. Les jeunes colonies vivent côte à côte avec d'autres espèces d'insectes utilisant le bois pourri comme nourriture ou, tels que les fourmis, comme abri. Une fois établies, les colonies paraissent ne subir que peu de pertes à la suite d'influences défavorables ou de prédateurs ; chose curieuse, elles ne sont pas recherchées par les pics.

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THE SINGLE STRAIN OF THE EGYPTIAN HONEYBEE, *APIS MELLIFICA FASCIATA* LATR.

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1°. Introduction.

Vogel (1865) and Rotter (1921) stated that there are half-queens which live together with the mother-queen in the hives of the Egyptian honeybee, *Apis mellifica fasciata* Latr. In a previous paper it could be proved that these half-queens did not exist in the Egyptian honeybee colonies in both Lower- and Upper-Egypt. (Kaschef, 1959 c.)

Rotter (1921) stated also that the Egyptian honeybee *Apis mellifica fasciata* Latr. is of different strains and that the honeybee of Upper-Egypt is more primitive than that of Lower-Egypt. He stated in page 9: "Die von Vogel und mir in *Fasciata*-Völkern konstatierten mysteriösen Wesen, welche Vogel „Halbköniginnen" benannte, hat Dr. Gough nicht erwähnt und ist demnach anzunehmen, dass er diese Feststellung nicht machte. Da ich nicht glauben kann, dass ihn eine derartige wichtige und rätselhafte Begebenheit entgangen wäre, vermute ich, dass die ägyptische Biene in dieser Hinsicht verschieden geartet ist und die Biene in Oberägypten noch ursprünglicher ist als die Biene in Unterägypten und Dr. Gough möglicherweise nur bei letzterer Beobachtungen anstellte."

The purpose of the present paper is to investigate whether one or more strains of *Apis mellifica fasciata* Latr. exist in Egypt. It is also hoped to obtain some information about the question of the variability of the tongue length of the Egyptian honeybee.

The author expresses his gratitude to Prof. Dr. M. T. Sayed for facilities offered during the course of this study.

2°. Material and Method.

The material used are ten colonies of *Apis mellifica fasciata* Latr. obtained from Lower- and Upper-Egypt: El-Mansûra, Shibin El Kôm, Kalyûb, Beni-Suef, El Minya, Sohag and Luxor. Samples of the Egyptian honeybee were also obtained from other different apiaries. Details of the methods and technique are given in the text.

For the investigation of the insect strains biological, anatomical and biometrical studies are necessary.

3°. Biological studies.

1°. **Weight.**—EXPERIMENT 1.—Newly emerged queens, workers and drones of *Apis mellifica fasciata* Latr. were weighed in groups or singly and the mean individual weight was calculated. The bees were normally weighed when 0-6 hours old. A summary of the results is given in table 1.

Table 1: Weights of newly emerged queens, workers and drones of *Apis mellifica fasciata* Latr. from Lower- and Upper-Egypt reared in observation hives.

WEIGHT (in mgms) of <i>Apis mellifica fasciata</i> Latr. FROM									
	MANSURA.			BENI-SUEF.			LUXOR.		
	Num- ber of bees weigh- ed.	Range.	Mean.	Num- ber of bees weigh- ed.	Range.	Mean.	Num- ber of bees weigh- ed.	Range.	Mean.
Queen	30	101-160	127.4 \pm 1.9	30	97-151	131.1 \pm 1.7	32	105-148	125.5 \pm 1.7
Worker	500	61-97	84.6 \pm 1.0	500	70-99	91.2 \pm 0.6	500	67-104	86.6 \pm 0.6
Drone	300	174-226	201.3 \pm 1.6	300	168-219	195.8 \pm 1.9	300	180-220	204.9 \pm 1.8

It appears from table I that though the weights of the three castes of *Apis fasciata* obtained from Mansûra, Beni-Suef and Luxor vary from 97 to 160 mgms for the queens, from 61 to 104 for the workers and from 168 to 226 mgms for the drones, the differences in the mean weights are small and doubtfully significant. The curves (Fig. 1) for each caste have been combined.

2°. **Length of the life-cycle.** — EXPERIMENT 2. — The duration of the developmental stages of each of the three castes of the Egyptian honeybee from both Lower- and Upper-Egypt were investigated in observation hives. For this purpose two colonies from each of Mansûra,

Beni-Suef and Luxor were used. Maps having hexagonal cells were drawn for the right and left sides of both the lower and the upper frames. In the case of workers and drones areas of not less than 100 cells were marked on the maps and examined daily from the time of egg laying until emergence. Special marks (—, +, (, 0) of different colours were used to distinguish the cells containing the larvae which are capped and the imagines which emerge on successive days. To investigate the

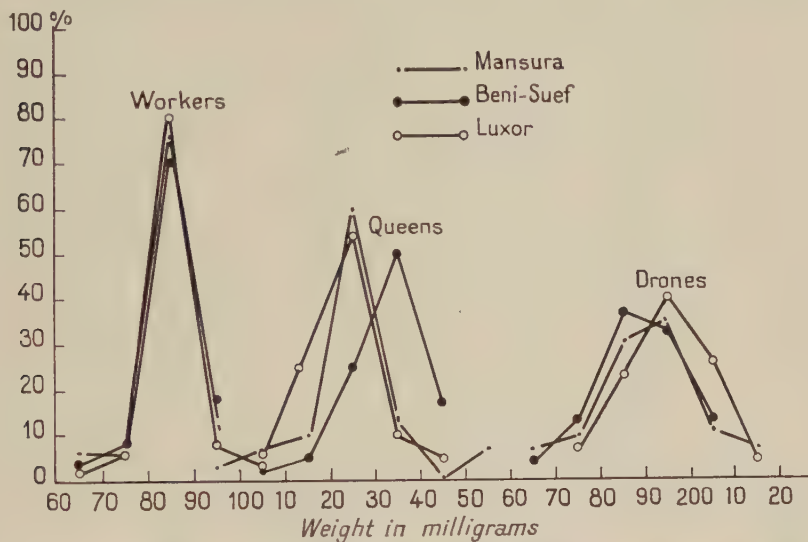


FIG. 1. — Frequency distribution of weights of *Apis mellifica fasciata* Latr. from Lower- and Upper-Egypt. The frequencies are expressed in percents.

durations of the developmental periods of the queens, removal of the original queen from the hive was adapted. To avoid the destruction of the other queen cells on the emergence of the first queen, the whole combs were transferred to an incubator of $32 \pm 0.5^\circ \text{C}$ and $60 \pm 5\%$ R. H. The length of the life-cycle from oviposition to the emergence of the adults outside the cells are shown in table 2 and figure 2.

Table 2 clearly shows that there is a wide spread in the emergence periods which is quite characteristic of honeybees and which is mainly due to individual differences as well as differences in the honeyflow, temperature of the comb and some other factors. The length of the life-cycles of the three castes of *Apis mellifica fasciata* Latr. from Lower- and Upper-Egypt are almost equal. The mean length of the life-cycles of the queens from Beni-Suef (14.91 ± 0.003 days) is somewhat shorter than those of the queens from Mansûra (15.82 ± 0.030 days) and Luxor (15.93 ± 0.031 days). There is also a difference of about one day between the mean duration of the life-cycles of the drones from Lower-Egypt (24.27 ± 0.027 days) and those from Upper-Egypt (25.52 ± 0.006



FIG. 2. — Length of Life-cycle of *Apis mellifica fasciata* Latr. from Lower- and Upper-Egypt.

and 25.62 ± 0.012 days respectively). But such differences which do not exceed one day are doubtfully significant.

TABLE 2. — LENGTH OF LIFE-CYCLE OF *Apis mellifica fasciata* Latr. FROM LOWER- AND UPPER-EGYPT (May-July 1957).

		DURATION (in days) OF THE LIFE-CYCLE OF <i>Apis fasciata</i> FROM					
		MANSURA.		BENI-SUEF.		LUXOR.	
		Range.	Mean.	Range.	Mean.	Range.	Mean.
Queen	Incubation period	3-3.5	$3.10 \pm .013$	2.9-3.5	$3.08 \pm .003$	2.9-3.5	$3.04 \pm .024$
	Larval period	3-5	$4.50 \pm .046$	4-6	$4.35 \pm .022$	4-6	$4.81 \pm .014$
	Pupal period	7-9	$8.32 \pm .032$	6-9	$7.40 \pm .005$	7-10	$8.08 \pm .054$
	Total	14-17	$15.92 \pm .030$	14-18	$14.91 \pm .003$	14-18	$15.93 \pm .031$
Worker	Incubation period	3-5	$3.23 \pm .050$	3-6	$3.16 \pm .042$	3-4	$3.20 \pm .021$
	Larval period	4-7	$5.01 \pm .031$	3-7	$4.97 \pm .093$	3-9	$5.04 \pm .038$
	Pupal period	8-15	$12.21 \pm .033$	9-15	$12.08 \pm .042$	8-14	$11.70 \pm .016$
	Total	16-24	$20.45 \pm .038$	16-23	$20.21 \pm .059$	17-24	19.94 ± 0.25
Drone	Incubation period	4-6	$5.27 \pm .002$	3-6	$5.18 \pm .001$	3-7	$5.23 \pm .007$
	Larval period	4-7	$5.98 \pm .013$	4-8	$6.03 \pm .014$	4-8	$6.17 \pm .016$
	Pupal period	11-17	$13.02 \pm .065$	11-16	$14.31 \pm .004$	11-15	$14.25 \pm .013$
	Total	20-28	$24.27 \pm .027$	20-29	$25.52 \pm .006$	19-28	$25.65 \pm .012$

3°. *Longevity*.—EXPERIMENT 3.—The investigation of the length of life of *Apis mellifica fasciata* Latr. from Lower- and Upper-Egypt was carried out on workers living in six normally breeding queen-right colonies used in the preceeding experiment. Fifty newly emerged workers from each colony were marked (v. Frisch, 1923) and liberated in their hives. The workers remaining alive were counted daily. The results of this experiment are shown in table 3 and illustrated by Fig. 3.

It appears from table 3 that the mean durations of hive-work life of *Apis mellifica fasciata* Latr. from Mansûra, Beni-Suef and Luxor were 19.53 ± 0.13 , 18.60 ± 0.47 and 20.66 ± 0.33 days respectively. The mean durations of the foraging life of the same workers were 13.90 ± 0.66 , 14.45 ± 0.15 and 13.35 ± 0.29 days respectively. The mean length of life of *Apis mellifica fasciata* workers from the three different districts

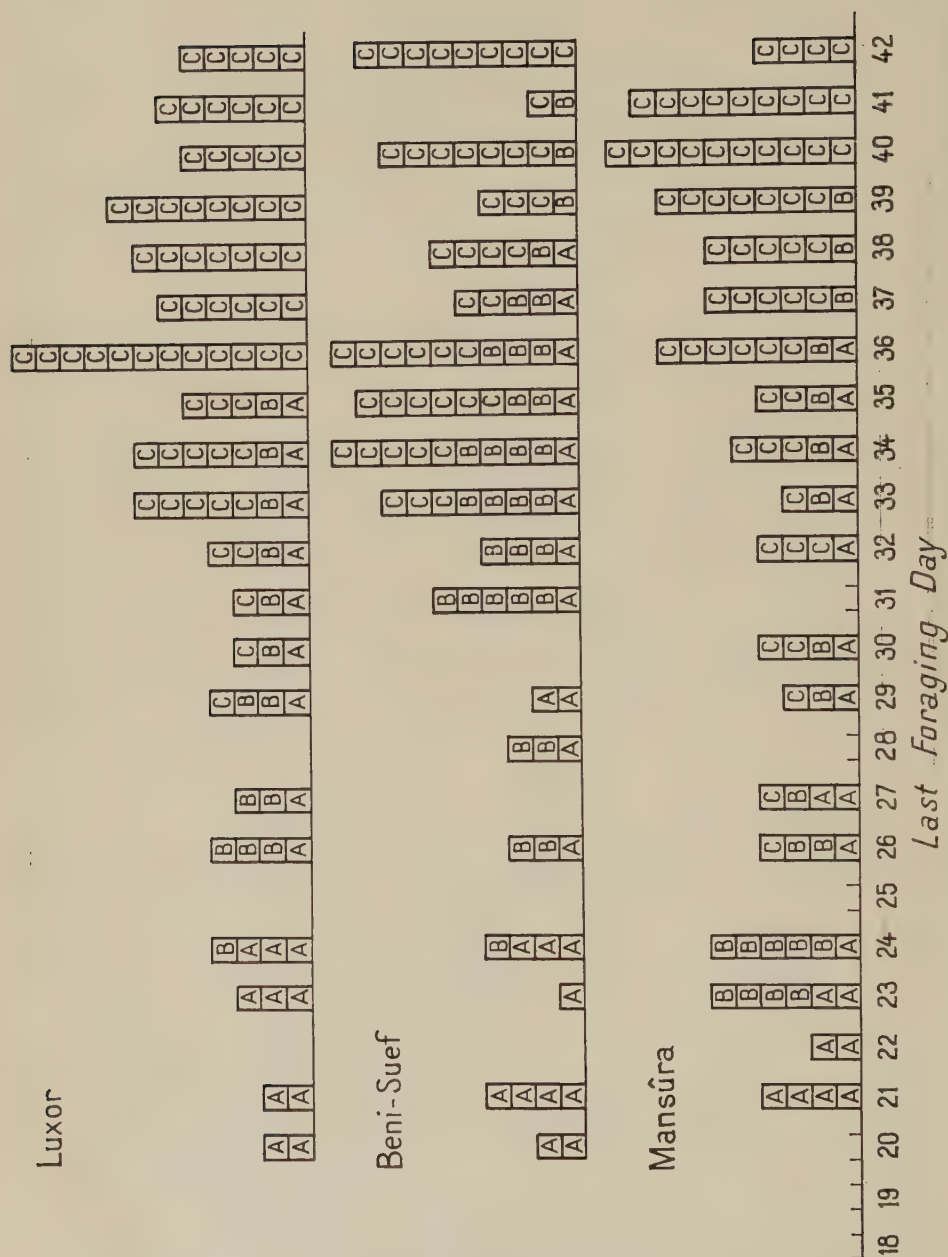


FIG. 3. — Longevity of *Apis mellifica fasciata* Latr. from Lower- and Upper-Egypt. Records of 100 bees from each of Mansûra, Beni-Suef and Luxor. A = bees which commenced foraging when 8 to 14 days old. B = bees which commenced foraging when 15 to 19 days old. C = bees which commenced foraging when 20 to 26 days old.

TABLE 3. — LONGEVITY OF WORKERS OF *Apis mellifica fasciata* Latr. FROM LOWER- AND UPPER-EGYPT.

	<i>Apis mellifica fasciata</i> Latr. FROM.						
	COLONY NUMBER.	MANSURA.		BENI-SUEF.		LUXOR.	
		Range.	Mean.	Range.	Mean.	Range.	Mean.
Length of hive-work life in days	1	13-26	$19.53 \pm .13$	12-25	$18.60 \pm .47$	9-26	$20.66 \pm .33$
	2	8-25		11-24		15-26	
Length of foraging life in days	1	13-25	$13.90 \pm .66$	9-16	$14.45 \pm .15$	8-15	$13.35 \pm .29$
	2	12-16		10-16		9-16	
Longevity in days			$33.43 \pm .79$		$33.05 \pm .62$		$34.01 \pm .62$

are 33.43 ± 0.79 , 33.05 ± 0.62 and 34.01 ± 0.62 days respectively. These results show that the mean longevity of the Egyptian honeybee workers from Lower- and Upper-Egypt is almost the same; differences between them are not significant.

TABLE 4. — NUMBER OF WORKERS OF *Apis mellifica fasciata* Latr. FROM LOWER- AND UPPER-EGYPT SURVIVING FOR 0.5-2 DAYS AT 32°C AND 60 % R. H.

RESISTANCE TO STARVATION IN DAYS.	NUMBER OF WORKERS DEAD.		
	<i>Apis mellifica fasciata</i> Latr. from		
	Mansûra.	Beni-Suef.	Luxor.
0.5	111	116	109
1	54	60	62
1.5	35	24	29
2	0	0	0
Mean	0.81	0.82	0.80

4°. *Resistance to starvation.*—EXPERIMENT 4.—The workers used in this experiment were also obtained from the same six colonies used

in the investigation of the duration of the developmental periods. More than 2000 newly emerged workers were marked and left in their hives for 18-20 days. Then one hundred workers from each hive were captured, made up into groups of five and each group was placed in a glass jar of 3.8×2 -in. with a filter paper of 3.5-in. in diameter on its base. The jars were placed in an incubator of 32°C and 60 % R. H. They were examined daily and the dead workers were removed and counted. The results are given in table 4.

Table 4 clearly shows that the workers of the Egyptian honeybee from Mansûra, Beni-Suef and Luxor equally tolerate starvation. Hence it is concluded that *Apis mellifica fasciata* Latr. from both Lower- and Upper-Egypt are equally resistant to starvation.

4°. Anatomical studies.

Number of ovarioles.—The number of ovarioles of newly emerging queens of *Apis mellifica fasciata* Latr. from Mansûra, Beni-Suef and Luxor is counted and the mean numbers are given in table 5.

TABLE 5. — NUMBER OF OVARIOLES OF VIRGIN QUEENS OF *Apis mellifica fasciata* Latr.

<i>Apis fasciata</i> from.	MEAN NUMBER OF OVARIOLES.		
	Left ovary.	Right ovary.	Left and right ovaries.
Mansûra	89.04 ± 4.91	92.60 ± 4.36	181.64 ± 9.27
Beni-Suef	96.13 ± 3.72	92.25 ± 5.29	188.38 ± 9.01
Luxor	91.76 ± 5.44	99.53 ± 4.38	191.29 ± 9.82

The mean number of ovarioles is 181.64 ± 9.27 , 188.38 ± 9.01 and 191.29 ± 9.82 for virgin queens of *Apis fasciata* from Mansûra, Beni-Suef and Luxor respectively. In each of the three samples examined, nevertheless, there is a wide range of variation in the number of ovarioles, which is characteristic of honeybees queens. However, the differences between the three samples in the mean number of ovarioles are not significant.

5°. Biometric studies.

Certain parts of the body of the workers of *Apis mellifica fasciata* Latr. from Lower- and Upper-Egypt were measured. The measurements were carried out on more than 3000 workers and drones from seven different Egyptian districts shown in Figure 4.

The technique used by Alpatov (1929) was adopted in measuring the different organs. Slightly anaesthetised workers were killed into boiling water to ensure complete extension of the proboscis. The dissected parts

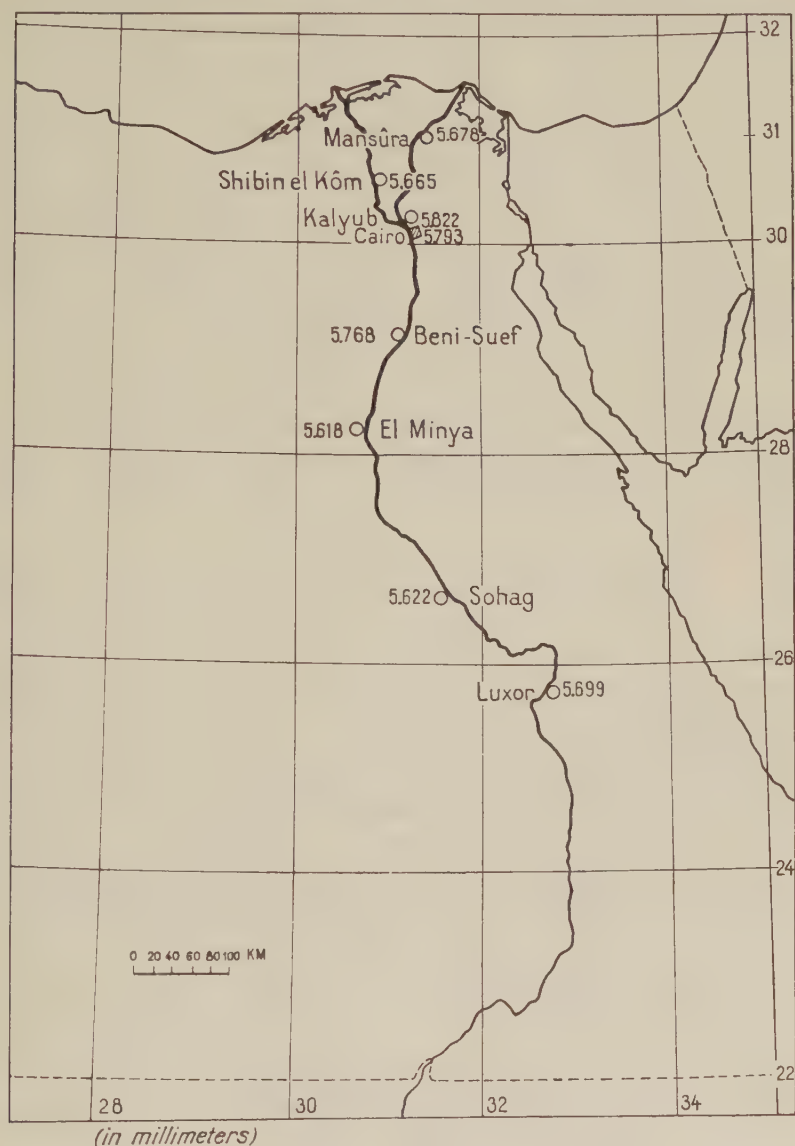


FIG. 4. — Distribution of average tongue length of *Apis mellifica fasciata* Latr. in Egypt.

were measured in water, and glycerin jelly was used as a medium for preservation.

Of the characters which have biological importance to the workers of honeybees and are consequently important to the bee-keepers:

- a. Length of the flagellum;
- b. Length of the tongue;
- c. Length of the tibia;
- d. Length and width of the basitarsus of the hind leg;
- e. Length, width and cubital index of the fore wing;
- f. Number of hooks on the hind wing;
- g. Length of the third sternum;
- h. Length and width of the first wax gland.

The dimensions of the fore wing, its cubital index, the number of hooks on the hind wing and the weight of newly emerging drones were also calculated.

The results of the measurements are summarised in tables 6 and 7. There appears to be no discontinuous morphological differences between the workers or between the drones of both Lower- and Upper-Egypt. There are no characters in which the means are widely different.

TABLE 7. — BIOMETRIC STUDIES AND WEIGHTS OF DRONES OF *Apis mellifica fasciata* Latr. FROM SEVEN DIFFERENT DISTRICTS IN LOWER- AND UPPER-EGYPT.

<i>Apis fasciata</i> from.	FORE WING.			HIND WING. Number of hooks.	WEIGHT (mgm).
	L (mm).	W (mm).	Cubital index (mm).		
Mansûra	11.1241 ± 0.0234	3.6072 ± 0.0372	1.5934 ± 0.0469	22.14 ± 0.044	216.127 ± 0.970
Shibin					
El Kôm	11.2034 ± 0.0351	3.6809 ± 0.0072	1.6115 ± 0.0309	21.23 ± 0.025	219.338 ± 1.044
Kalyûb	11.4729 ± 0.0065	3.6981 ± 0.0094	1.6988 ± 0.0064	22.40 ± 0.005	215.971 ± 1.107
Beni-					
Suef	11.2646 ± 0.0078	3.6322 ± 0.0405	1.6403 ± 0.0081	21.67 ± 0.005	217.720 ± 0.943
El					
Minya	11.3458 ± 0.0197	3.6247 ± 0.0265	1.6352 ± 0.0264	22.61 ± 0.046	216.545 ± 0.899
Sohag	11.3797 ± 0.0088	3.6715 ± 0.0078	1.6761 ± 0.0191	22.55 ± 0.025	217.565 ± 0.781
Luxor	11.1980 ± 0.0086	3.6774 ± 0.0070	1.6649 ± 0.0062	22.44 ± 0.032	218.686 ± 0.914
Mean	11.2844 ± 0.0157	3.6560 ± 0.0194	1.6457 ± 0.0206	22.15 ± 0.029	217.422 ± 0.971

6°.—Variability in the tongue length.

In the course of this work the attention of the author was attracted to the question of the variability in the tongue length of the honeybee by the article of Micailov (1924) who pointed out that the length of the bees in plain of European Russia increases regularly from the North to the South. Figure 5 shows the distribution of the average tongue length (in millimeters) of *Apis mellifica fasciata* Latr. in Egypt. Table 8 shows

that the mean length of the workers tongue is nearly uniform in Lower- and Upper-Egypt.

TABLE 8. — FREQUENCIES AND MEANS OF THE TONGUE LENGTH OF *Apis mellifica fasciata* Latr. FROM SEVEN DIFFERENT DISTRICTS IN LOWER- AND UPPER-EGYPT.

TONGUE LENGTH (mm).	PERCENTAGE FREQUENCY DISTRIBUTION OF <i>Apis fasciata</i> WORKERS FROM							SUM
	Man- sûra.	Shibin El Kôm	Kalyûb.	Beni- Suef.	El Minya.	Sohag.	Luxor.	
5.230-5.329					6	2		8
5.330-5.429	2	4			2	2	2	12
5.430-5.529	3	6	2		6	12	2	31
5.530-5.629	15	31	0	2	20	46	22	136
5.630-5.729	48	34	26	40	50	26	56	280
5.730-5.829	24	10	44	28	8	10	10	134
5.830-5.929	7	11	18	30	6	2	8	82
5.930-6.029	1	4	8		2			15
6.030-6.129			2					2
Mean	5.678 ± 0.048	5.665 ± 0.046	5.822 ± 0.069	5.768 ± 0.029	5.618 ± 0.016	5.622 ± 0.005	5.699 ± 0.013	5.7139 ± 0.0078

The main sources of nectar, which are the flowers of clover, cotton and maize, are one and the same in both Lower- and Upper-Egypt. Thus, one should expect to find no significant differences in the lengths of the tongues of *Apis fasciata* workers brought from either the South or the North; a conclusion which is concordant with the results obtained in this work. Such differences may occur if the bees from the different localities utilise different flowers with different nectar levels in the corollas.

Concerning the variation in the tongue length of the Egyptian honeybee in the limits of a given apiary, figure 6 gives the frequency curves of workers belonging to six different colonies of *Apis fasciata* from the neighbourhood of Cairo (Kalyûb). The results obtained show that the means of the single colonies (5.632 ± 0.009 , 5.725 ± 0.001 , 5.740 ± 0.009 , 5.877 ± 0.008 , 5.847 ± 0.011 and 5.859 ± 0.013 mms) do not differ considerably.

Summary.

1. One strain occur only in *Apis mellifica fasciata* Latr. which dominates Lower- and Upper-Egypt. This contradicts Rotter's hypothesis (1921)

in which he supposed that the Egyptian honey-bee is of different strains and that the honeybee of Upper-Egypt is more primitive than that of Lower-Egypt.

2. *Apis mellifica fasciata* Latr. obtained from seven different districts

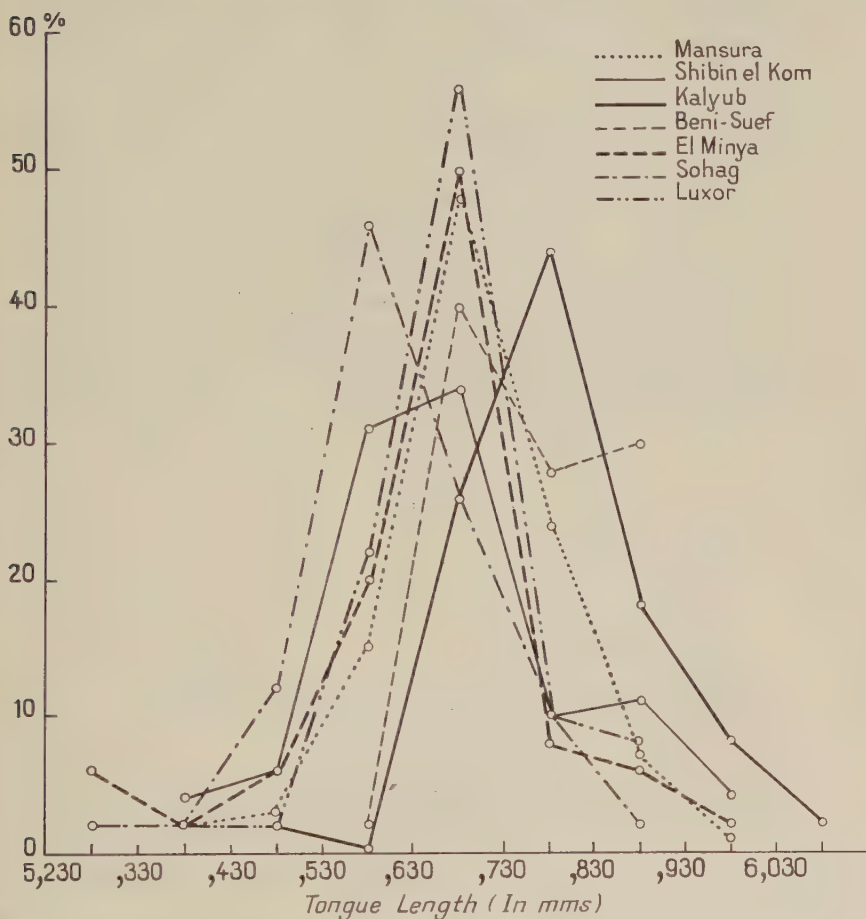


FIG. 5. — Frequency distribution of the tongue length of *Apis mellifica fasciata* Latr. from seven different Egyptian districts. The frequencies are expressed in percents.

are quite similar in the characters investigated; a) biological characters: body weight, length of the life-cycle, longevity and resistance to starvation, b) anatomical character: number of ovarioles of virgin queens, and c) morphological characters: length of the flagellum, length of the tongue, dimensions and cubital index of the fore-wing, number of hooks on the hind wing, length of the third sternum and dimensions of the first wax gland.

3. The tongue length of the workers of the Egyptian honeybee is more

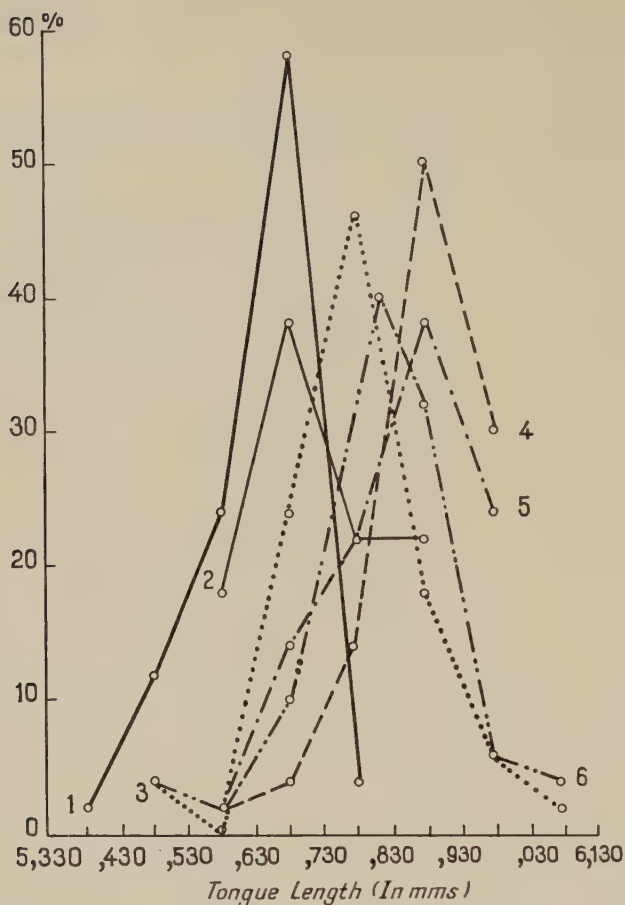


FIG. 6. — *Apis mellifica fasciata* Latr. Variation curves of tongue length of six colonies from the neighbourhood of Cairo. The frequencies are expressed in percents.

or less uniform in Lower- and Upper-Egypt. It does not differ also considerably in a given apiary.

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LES NIDS DE *GLOBITERMES SULPHUREUS* HAVILAND AU CAMBODGE

par CH. NOIROT

Globitermes sulphureus est très répandu en Malaisie et en Indochine (*G. annamensis* Desneux doit être synonyme, d'après Snyder, 1949), mais nous savons peu de chose sur sa biologie. Le nid a été sommairement décrit par Bathellier (1927); nous sommes encore plus mal renseignés sur les autres espèces de ce genre indo-malais.

Au Cambodge, *G. sulphureus* est très fréquent. Nous l'avons récolté, d'une part, aux environs de Kep (S. W. de Phnom-Penh, au bord du golfe de Siam), d'autre part, dans la région de Kompong-speu (50 km à l'ouest de Phnom-Penh), en zone de rizières. En outre, nous avons aperçu, dans les plantations d'hévéas de Chup (100 km à l'est de Phnom-Penh), des nids construits très probablement par la même espèce. Sa présence au Cambodge avait d'ailleurs été signalée par Bathellier (1927), mais sans indications plus précises. Nous avons pu faire, sur les constructions de ce Terme, quelques observations, malheureusement trop rapides, qui montrent pourtant tout l'intérêt de cette espèce.

1^o Structure du nid.

Sous sa forme achevée, le nid de *G. sulphureus* possède une structure complexe, exceptionnelle dans la sous-famille des Amitermitinæ.

Voici la description d'un grand nid, exploré le 26 juin 1956, près de Kep (bord du golfe de Siam); dans la même région, deux autres nids, rapidement examinés, nous ont montré des structures identiques. L'édifice en question était situé dans une forêt secondaire, sur une colline en pente assez forte tournée vers la mer. Il s'agit d'un dôme aigu (fig. 1), dont la hauteur est de 90 cm (mesurée depuis le bas de la pente) et la largeur à la base de 65 cm; il comporte extérieurement une mince *écorce* en matériaux terreux (épaisseur 5 à 6 mm), fragile, continue et bien individualisée sur toute la surface du nid. Cette écorce adhère à la *muraille* sous-jacente par des piliers coniques, dont la base fait partie de la muraille et la pointe est soudée à l'écorce; çà et là se voient des adhérences plus larges. Sous l'écorce, la surface externe de la muraille est irrégulière; ainsi se trouve délimité, entre l'écorce et la muraille, un espace continu qui rappelle à bien des égards la *paraécie* de beaucoup de Macrotermitinæ et de certains Apico-

termes. Faute de connaître le développement du nid, nous ne pouvons pas préjuger de l'homologie de ces structures, mais, à titre purement descriptif, nous utiliserons le terme de *paraécie* pour l'espace périphérique du nid de *Globitermes sulphureus*. Au niveau du sol, l'écorce disparaît, se soudant à la terre environnante, mais la paraécie se prolonge sur une profondeur de 20 cm environ, limitée extérieurement par le sol, intérieurement par la

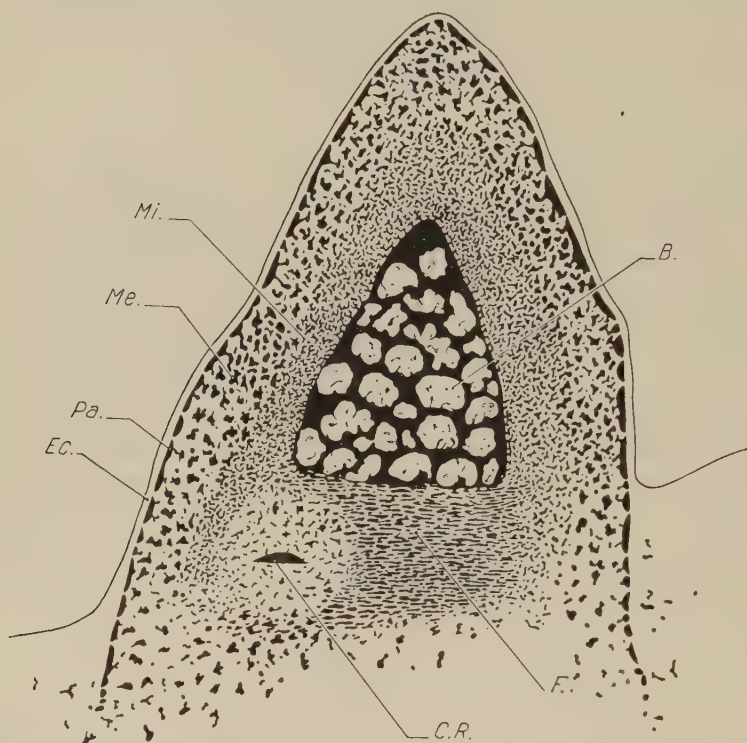


FIG. 1. — Coupe du nid de *Globitermes sulphureus*. B., boules ou amas de bois aggloméré (matières de réserves) remplissant la cavité centrale ; C. R., cellule royale au sein d'un nodule compact ; EC., écorce ; F., construction feuilletée ; Me., zone externe de la muraille ; Mi., zone interne de la muraille ; Pa., paraécie (espace séparant l'écorce de la muraille).

muraille ; comme dans la partie épigée, elle est traversée de piliers coniques partant de la muraille.

La muraille elle-même est épaisse de 15 à 20 cm et formée de deux zones bien distinctes. La zone externe est grossière, creusée de galeries s'élargissant en larges chambres irrégulières dépassant souvent 2 cm de diamètre, aux parois épaisses (jusqu'à 3 cm). Ce système de cavité communique avec la paraécie par de nombreuses galeries, généralement étroites (2 à 3 mm), parfois beaucoup plus larges (10 à 15 mm). Le matériau est compact, dur mais cassant, paraissant formé de fins éléments terreux avec un peu de carton stercoral ; la surface des chambres et des galeries est tapissée d'un enduit lisse brun noirâtre. Vers l'intérieur, on passe progressivement,

mais rapidement, à la *zone interne*, moins massive, creusée d'un réseau beaucoup plus dense de galeries et de chambres plus petites (galeries ayant 2 à 4 mm de diamètre, chambres ne dépassant pas 10 mm de largeur), aux parois plus minces (1 à 8 mm); le matériau est du même type que dans la partie externe, mais paraît contenir une plus forte proportion de carton de bois; le même enduit brun noirâtre recouvre les parois.

Cette muraille se prolonge, avec la même structure, au-dessous du niveau du sol, jusqu'à une profondeur d'une vingtaine de centimètres, restant séparée de la terre environnante par la paraécie, puis se confond peu à peu avec le sol qui est parcouru par un réseau de galeries, souvent assez larges, aux parois plus ou moins maçonnées.

À l'intérieur de la muraille, la base du nid est remplie par une construction feuilletée très délicate formée de minces lamelles de carton de bois (épaisseur 0,4 à 2 mm), irrégulières, mais à direction générale horizontale, se soudant par places les unes aux autres et délimitant ainsi des chambres plates, très irrégulières, dont la hauteur varie de 2,5 à 7 mm. Ce feuilleté occupe la zone voisine de la surface du sol (F. fig. 1), mais sur un côté (dans l'exemple étudié, vers le bas de la pente) il est remplacé par un gros nodule en carton de bois compact. Ce nodule se présente comme une excroissance de la muraille, et le passage entre les deux structures est progressif : remplacement de plus en plus complet de la terre par le carton de bois, diminution de la densité et du diamètre des galeries et des chambres; vers le centre, au contraire, le passage au feuilleté précédent est brusque, bien qu'il y ait continuité entre les deux types de construction. Au centre de ce nodule, se tient la *cellule royale*, de forme lenticulaire, le plafond étant plus bombé que le plancher; d'un contour à peu près circulaire, la cellule royale a un diamètre de 75 mm, et une hauteur maximum de 15 mm. La périphérie et le plafond montrent des orifices assez nombreux, larges de 1 à 2 mm, tandis que le plancher en présente peu.

Au-dessus de la construction feuilletée et du nodule contenant la chambre royale, le centre du nid est une cavité, grosse comme une tête d'enfant, *non cloisonnée*, presque entièrement remplie par des formations très particulières; il s'agit de masses mesurant de 4 à 8 cm de diamètre maximum, de couleur bistre foncé et de forme assez variable, souvent globuleuse, parfois très irrégulière. Le plus souvent, la face supérieure a un relief beaucoup moins tourmenté que la face inférieure (fig. 1 et 2, pl. I). Ces masses ne sont pas soudées les unes aux autres, ni à la paroi, mais simplement empilées dans la cavité centrale. La texture de ces amas est compacte, mais l'examen à la loupe permet de reconnaître une structure oolithique très serrée: ils sont formés de boulettes étroitement soudées les unes aux autres, chaque boulette ayant un diamètre voisin de 0,4 mm et représentant sans doute l'apport d'un ouvrier. La nature de ce matériau est très difficile à définir par la seule observation; la texture oolithique, la légèreté relative de ces masses font songer à des éléments végétaux finement broyés et non à du carton stercoral (voir plus loin).

2° Variations dans la structure du nid.

L'architecture que nous avons décrite est sans doute la règle dans cette espèce ; en effet, la description rapide que donne Bathellier (1927) correspond bien à nos observations (1), et il dit l'avoir observée en Annam, Cochinchine et Cambodge (sans autre précision malheureusement). En outre, dans les plantations d'hévéas de Chup, nous avons vu des nids tout à fait semblables extérieurement, mais nous n'avons pas eu la possibilité de les explorer. Notons pourtant que les nids de la forêt malaise, vus par John (1925), pourraient avoir une structure différente et paraissent en partie souterrains ; mais la description de John est trop sommaire pour nous permettre une comparaison utile.

En revanche, dans les rizières du Mékong, et notamment dans la région de Kompong-speu, nous n'avons observé aucun nid de ce type, pourtant facile à repérer. Cependant *Globitermes sulphureus* y paraît fréquent ; une première capture (ouvriers et soldats) en fut faite dans la muraille d'une grande termitière de *Macrotermes gilvus* abandonnée, dans des galeries tapissées d'un enduit brun noirâtre ; aucune construction épigée n'était visible dans le voisinage (sauf d'autres nids de *M. gilvus*), le nid devait être entièrement souterrain. Un peu plus loin, nous avons observé *G. sulphureus* dans un petit édifice bien différent du grand nid précédemment décrit : c'était un cylindre irrégulier, d'aspect ruiniforme, haut d'environ 25 cm et adossé au tronc d'un arbuste. La structure ne rappelait que de très loin celle des nids typiques : une muraille terreuse, très grossière, à surface érodée, d'une épaisseur voisine de 5 cm, recouvrait des amas très analogues aux boules de réserves précédemment décrites, mais ayant par places une couleur noirâtre ; dans le sol, la construction s'arrêtait à faible profondeur (5-10 cm). L'ensemble épigé ne constituait certainement pas la totalité de la termitière, car, si la population y était très dense, elle consistait surtout en ouvriers et soldats, les larves y étaient très peu nombreuses. Probablement, le centre du nid était situé ailleurs dans le sol.

Notre exploration a été bien trop brève pour que nous puissions dire que les nids épigés typiques n'existent pas en zone de rizières, mais nous pouvons affirmer que, dans ce milieu particulier, *Globitermes sulphureus* peut se contenter d'un habitat souterrain ou de constructions épigées rudimentaires. Il est possible que, dans ces régions non boisées, la violence des pluies entrave la construction aérienne, tandis que, sous un couvert, même clairsemé, les feuilles des arbres protègent l'édifice assez fragile du choc direct des gouttes d'eau.

Comme dans le cas de *Macrotermes gilvus*, se pose le problème de l'adaptation de l'espèce à des milieux très différents (Noirot, 1959).

(1) Bathellier ne décrit pas les amas remplissant la cavité centrale, mais le schéma qu'il donne laisse à penser qu'elles étaient présentes dans les nids qu'il a étudiés.

3° Les matériaux constituant le nid.

La simple observation nous montre que le nid n'a pas une constitution homogène dans toutes ses parties, que plusieurs types de matériaux interviennent dans la construction. Quelques dosages très simples vont nous permettre de serrer le problème de plus près.

Nous avons mesuré, d'une part, la teneur en matières minérales et organiques, d'autre part, la teneur en lignine et en cellulose des différentes parties du nid. La matière minérale est évaluée simplement par calcination ; cette méthode est certes très grossière, mais elle nous suffit, eu égard à l'importance des différences constatées. La lignine est dosée suivant la méthode de Hagglund, la cellulose par la méthode de Kurehner et Hoffer ; là encore, on ne saurait obtenir des chiffres très précis. Les résultats, consignés dans le tableau I, aboutissent pourtant à des conclusions cohérentes.

TABLEAU I.

	CENDRES. (p. 100)	LIGNINE. (p. 100)	CELLULOSE. (p. 100)	RAPPORT LIGNINE- CELLULOSE.
Muraille, zone externe	81,2	12,7		
Muraille, zone moyenne	59,3	32		
Muraille, zone interne	22,7	47,1	12,8	3,7
Cellule royale	18,2	49,3	19,5	2,5
Construction feuilletée	9,3	39,8	29,3	1,36
Boules de la cavité centrale.	4,4	38,1	31,2	1,25

a) La teneur en matière organique augmente régulièrement de l'extérieur à l'intérieur. La progression peut être suivie en toute netteté dans la muraille, où la zone externe est essentiellement formée d'éléments minéraux, tandis que la zone tout à fait interne n'en compte guère plus de 20 p. 100 ; la région de la cellule royale fournit des chiffres très voisins, mais la teneur en matières organiques augmente dans le feuilleté central ; enfin, les boules énigmatiques sont remarquablement pauvres en éléments minéraux.

b) Les matières organiques incorporées à l'édifice varient non seulement d'une façon quantitative, mais aussi qualitative.

Dans la muraille, ces matières organiques sont formées essentiellement de « lignine », la cellulose est fort peu abondante (la teneur en éléments minéraux, dans les parties externes et moyennes de la muraille, est trop élevée pour qu'un dosage de cellulose ait une signification par la méthode utilisée) ; dans le nodule qui contient la cellule royale, la teneur en lignine est maximum, mais la cellulose est nettement plus abondante ; la teneur en cellulose devient beaucoup plus élevée dans le feuilleté et surtout

dans les boules de la cavité centrale, tandis que la teneur en lignine baisse nettement.

Nous pouvons interpréter ces résultats de la façon suivante : Les ouvriers de *Globitermes* utilisent 3 matériaux bien distincts :

1° La terre du sol environnant.

2° Leurs excréments, qui constituent le *carton stercoral* employé par un grand nombre de Termites.

3° Des débris végétaux non digérés, prélevés directement à l'extérieur. La teneur en matières minérales traduit directement la proportion de terre utilisée dans la construction; les teneurs relatives en lignine et en cellulose, qui varient beaucoup, s'expliquent par la coexistence des deux autres matériaux en proportions variables.

Bien que la physiologie digestive des Termites supérieurs nous reste très mal connue, nous savons qu'ils doivent utiliser la cellulose grâce à des bactéries symbiotiques (Hungate, 1946 ; Misra et Ranganathan, 1954 ; Pochon de Barjac et Roche, 1959 ; Grassé et Noirot, 1959), alors que la lignine n'est pas digérée (1). C'est pourquoi nous pensons que les matériaux organiques de la muraille sont de nature purement excrémentitielle ($\text{rapport } \frac{\text{lignine}}{\text{cellulose}} = 3,7$), alors qu'à l'opposé les boules de la cavité centrale sont essentiellement constituées de matière végétale brute ($\text{rapport } \frac{\text{lignine}}{\text{cellulose}} = 1,25$). Les autres parties du nid contiennent un mélange d'excréments et d'éléments non digérés; les excréments l'emportent dans la région de la cellule royale, mais n'ont qu'une faible importance dans le feuilleté central.

Cette interprétation est corroborée par l'examen microscopique. Une parcelle de région interne de la muraille, écrasée dans une goutte d'eau, se montre formée de débris extrêmement fins, dont le diamètre est presque toujours inférieur à 10μ (en général compris entre 2 et 7μ); les fragments plus gros sont rares, et ce n'est qu'exceptionnellement qu'on observe un fragment de fibre végétale reconnaissable. Au contraire, les masses centrales sont constituées de débris plus gros, dont le diamètre est généralement compris entre 15 et 30μ ; assez souvent, on observe des fragments de vaisseaux et surtout de fibres ligneux, atteignant 50 et même 100μ de longueur; les parois de la cellule royale montrent une constitution intermédiaire.

4° Discussion.

a) *Structure et croissance du nid.* — Parmi les cas connus actuellement, *Globitermes sulphureus* construit le nid le plus complexe de la sous-famille des Amitermitinæ; seul peut lui être comparé *Cephalotermes rectangularis*

(1) Chez les Macrotermitinæ, il est vraisemblable que la lignine est attaquée par le *Termitomyces* de la meule à champignon (Grassé et Noirot, 1958).

d'Afrique (Grassé, 1939), dont l'architecture, assez différente, atteint aussi un haut degré de perfection, qui n'est dépassé que par les *Apicotermes* et certains *Macrotermitinæ*.

La complexité du plan architectural s'accompagne d'un choix remarquable des matériaux, qui varient suivant la région de la Termitière; l'utilisation de la terre et du carton stercoral est banale chez les Termites, et en particulier les *Amitermitinæ*, mais l'incorporation de matière végétale non digérée n'avait pas été signalée jusqu'ici; rien ne prouve qu'il s'agisse d'un cas unique, car la structure et surtout la composition du nid de très nombreuses espèces ne sont encore connues que de façon très imparfaite.

Nous ne savons malheureusement pas comment prend naissance l'édifice du *Globitermes* et n'en connaissons que la forme adulte; l'ontogénèse de ce nid permettrait sans doute d'en mieux comprendre la signification et peut-être d'établir des homologues avec ce qu'on observe dans d'autres espèces (voir Grassé et Noirot, 1958); mais le problème de la croissance doit pour-tant être posé.

Si nous exceptons les boules qui remplissent la cavité centrale, toutes les parties du nid sont en continuité, réunies par des zones de transition. Il importe de voir dans ce nid une unité *dynamique*, qui se développe et s'accroît. Cette croissance apparaît comme un phénomène très complexe; elle ne peut se faire par simple adjonction de parties nouvelles, mais implique un remaniement de toute l'épaisseur de la muraille. Comme chaque partie du nid possède non seulement une architecture propre, mais aussi une proportion définie des divers matériaux, ces remaniements doivent être très profonds et impliquent, de la part des ouvriers, des ajustements du comportement extrêmement précis.

Le problème de la croissance du nid se pose de la même façon pour tous les Termites qui construisent un édifice ayant un plan défini; et l'on a noté à diverses reprises l'utilisation de matériaux différents pour les diverses zones du nid: les analyses faites par Cohen, 1933; Holdaway, 1933, chez *Nasutitermes exitiosus*, Grassé et Joly, 1941, chez *Amitermes evuncifer*, montrent que la périphérie du nid est faite surtout de terre, tandis que le centre est riche en matériaux stercoraux; la simple observation montre qu'il en est de même chez *Cornitermes cumulans* (Grassé, 1958); mais, chez *Globitermes*, l'utilisation d'un troisième matériau (débris végétaux mâchés) introduit un nouvel élément de complexité.

b) *Signification des amas centraux*. — Ces masses, constituées de débris végétaux non digérés, entassées au milieu du nid, n'ont certainement pas la même signification que les autres parties de la construction; nous n'y avons trouvé qu'une population très clairsemée, le couvain étant concentré dans la zone feuilletée sous-jacente. On est fortement tenté d'y voir des *réserves alimentaires*, et l'aspect irrégulièrement évidé de la face inférieure (fig. 2, pl. I) suggère qu'elle a pu être rongée par les Termites; en examinant soigneusement cette face inférieure, nous avons pu déceler des zones attaquées par les Termites, fraîchement érodées, mais ces zones

d'attaque sont relativement peu étendues. Nous ne connaissons pas le rôle exact de ces réserves alimentaires, mais elles représentent une masse importante : nous évaluons à 1 kg leur poids total dans le nid de *Globitermes* qui nous a servi d'exemple. Peut-être ces réserves sont-elles utilisées surtout à certaines saisons ?

Les réserves alimentaires s'observent rarement chez les *Amitermitinae* : *Amitermes laurensis*, *A. meridionalis* (Mjöberg, 1920 ; Hill, 1942), *A. vitiosus* (Hill, 1942), *Drepanotermes rubriceps* (Mjöberg, 1920), mais il s'agit dans ces quatre espèces de débris végétaux simplement entreposés dans certaines chambres du nid, comme on l'observe dans bien d'autres termitières (*Trinervitermes*, par exemple), et non de constructions bien définies.

Au contraire, *Microcerotermes depokensis* édifie dans son nid des boules de matière végétale (John, 1925 ; Kemner, 1934) qui rappellent de façon tout à fait frappante celles que bâtit *G. sulphureus* ; Kemner avait déjà noté que la face inférieure paraissait rongée par les Termites et a pu observer, en élevage, les ouvriers s'en nourrir ; aussi leur a-t-il attribué la signification de réserves alimentaires. En dehors des *Amitermitinae*, les *meules à champignons* des *Macrotermitinae* rappellent, par leur structure et leur composition, les boules construites par *G. sulphureus* ou *M. depokensis* ; nous avons montré (Grassé et Noirot, 1957, 1958) que ces meules à champignons étaient rongées par les Termites, mais après avoir subi, de la part du champignon, des modifications complexes ; leur rôle est donc assez différent. Avec *Sphaerotermes sphaerothorax*, seul *Macrotermitinae* dont les meules ne portent pas de champignons (Grassé et Noirot, 1949), la ressemblance est beaucoup plus nette, tant par la stérilité de ces « meules » que par leur aspect compact. Malgré les incertitudes qui règnent encore dans le rôle exact de ces diverses constructions, nous devons noter une convergence frappante dans le comportement de Termites taxinomiquement éloignés les uns des autres.

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Résumé.

Globitermes sulphureus construit normalement un nid complexe, obéissant à un plan rigoureux, qui est décrit en détail, mais semble pouvoir se contenter d'une architecture beaucoup plus simple dans des conditions écologiques particulières (zone des rizières).

Une attention particulière est donnée aux matériaux constituant le nid. Les observations et analyses permettent de conclure que ce Terme utilise trois matériaux distincts : terre du sol environnant, excréments (riches en lignine), bois ou autre matière végétale non digérée (où la cellulose est abondante). Chaque région du nid comporte une proportion définie de ces 3 éléments ; les matériaux terreux, prédominant à la périphérie, diminuent rapidement d'importance en allant vers l'intérieur ; les matières excrément-

tielles dominant dans la zone interne de la muraille, mais sont progressivement remplacées par le bois non digéré dans les régions plus internes.

Dans la cavité centrale du nid sont entassés des amas irréguliers constitués presque uniquement de débris de bois très fin solidement agglomérés; ces amas sont interprétés comme des réserves alimentaires.

Summary.

Globitermes sulphureus normally builds an intricate nest, following a strictly defined plan which is described in detail in this work. In particular ecological conditions, however, this architecture may be considerably simplified (rice marshland).

Particular attention has been paid to the types of material which make up the nest. Our observations and analyses lead to the conclusion that three distinct substances are used in the process: soil taken up from the environment, excremental matter (highly ligneous), wood or other non-assimilated fragments (rich in cellulose). Each area of the nest contains a specific proportion of these three elements: the earthen material, which predominates peripherally, decreases rapidly as one penetrates the nest; the inner side of the wall is mainly built of excremental matter, which, in the more internal regions, is progressively replaced by the non-assimilated vegetal material.

Irregular heaps almost entirely made of thin and thoroughly agglomerated fragments of wood are to be found in the central cavity of the nest: these are believed to be food reserves.

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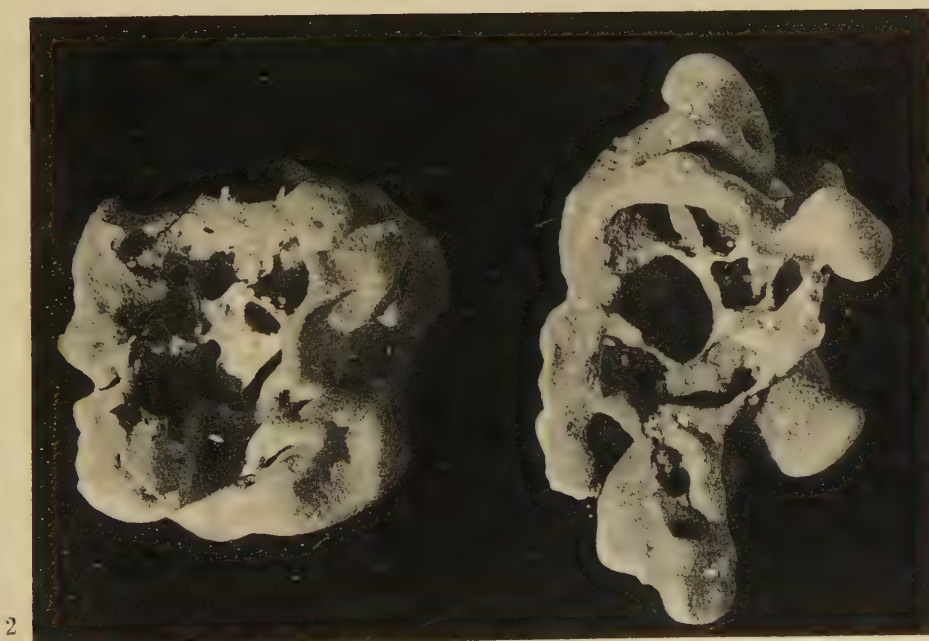
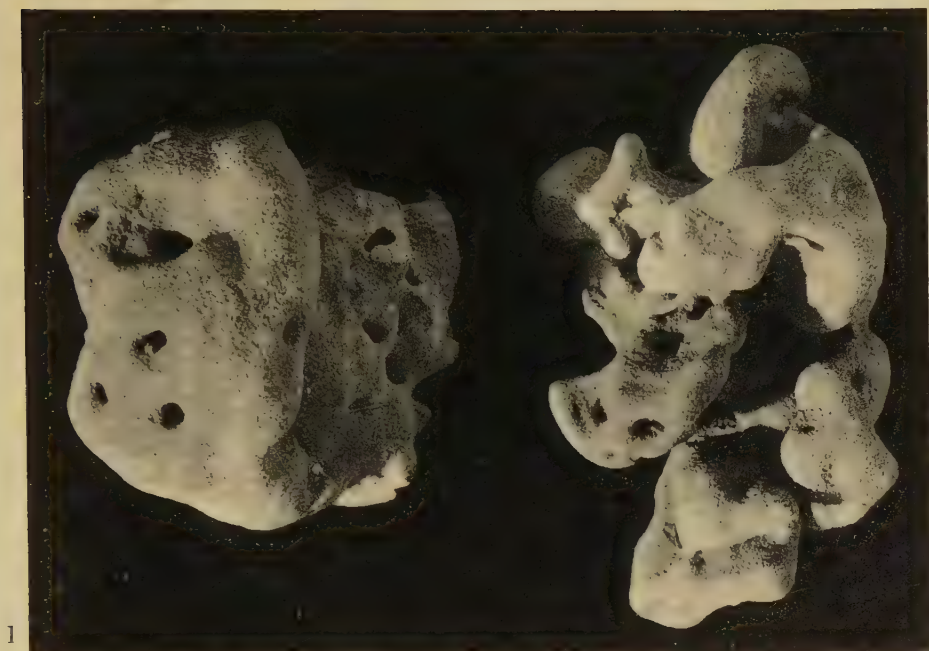
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LÉGENDE DE LA PLANCHE HORS TEXTE *

Amas de bois aggloméré, vus par leur face supérieure (1) et leur face inférieure (2); on a choisi un échantillon de forme bien régulière (à gauche) et un autre très irrégulier (à droite); on voit que la face inférieure (fig. 2) est évidée, rongée (grandeur naturelle).

(*) Les frais de fabrication de cette planche et des deux planches hors-texte parues dans le fascicule 2-1959, p. 185 ont été couverts par le *Laboratoire d'Évolution des Êtres Organisés de la Faculté des Sciences*.



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Globitermes sulphureus

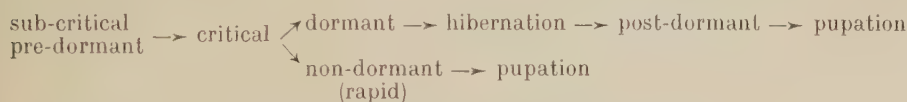
THE INFLUENCE OF WORKER AGE ON TROPHOGENIC LARVAL DORMANCY IN THE ANT MYRMICA

by J. S. WEIR

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INTRODUCTION

Third instar larvae of the ant *Myrmica* can develop in the summer of larval eclosion (*non-dormant* larvae, or rapid brood), but certain larvae overwinter (*dormant* larvae) and develop the following spring (*post-dormant* larvae). In a previous paper (Weir, 1959 *c*) a *critical stage* in larval development and in the condition of the retrocerebral endocrine system has been described. Larvae diverge from this critical stage to one or other of these developmental paths. Third instar larvae prior to this stage are designated *pre-dormant* or *sub-critical*. Larval relationships and terminology can be shown diagrammatically:



The present experiments investigate the determination of larvae for dormancy and non-dormancy (Brian, 1951, 1954, 1955 *b* ; Weir, 1959 *b*), and were undertaken during the years 1951-1954 in the Zoology Department at Glasgow University.

Material was collected from localities in the south-west of Scotland. The taxonomy of the species of ant used (*Myrmica rubra* L.) has been considered by Brian and Brian (1949, 1955) who have described the forms *M. rubra microgyna* and *M. rubra macrogyna*. Their nomenclature has been followed here.

METHODS

In the course of these experiments numerous larvae have been reared by workers under varying conditions. Anaesthesia was avoided as it is known to affect workers (Weir, 1957 *a*). The following measurements have been made on larvae.

The total larval area was measured by projection of the lateral view from a slide of standard depth, the larva being held under water by a coverslip. For small larvae this gives a rapid and accurate measurement of bulk.

Larval "girth" (i.e. weight/length or area/length). Girth was measured in preference to either length or weight, since early third instar larvae first elongate and then expand laterally in the course of growth and development.

The area of the residual food in the larval gut. This was measured by projection as for the total area. The area measured is the area enclosed by the secondary peritrophic membrane (Weir, 1957 *b*).

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The length of the larval malpighian tubules occupied by white crystalline material. (This material was not analysed. It is presumed to be crystalline uric acid.) The length of the individual tubules occupied was measured by projection, and summed for each larva. In *Myrmica* larvae both the length and width of that section of the tubule which is filled with white crystals are variable. This is not always the case, e.g. *Rhodnius* (Wigglesworth, 1953).

The apportionment of the brain between the head capsule and the larval prothorax. Microscopic examination of larvae in side view under water on a slide of standard depth showed that the position of the brain varied with the state of development, as described also in dormant and post-dormant larvae (Brian, 1954). Measurements were made of that percentage of the brain which lies behind the posterior border of the head capsule (Weir, 1959 c, fig. 1). It seems possible that this movement is caused either: by the degree of turgor of the body during development (it has been shown that the degree of movement of the brain may be affected by the degree of hydration of the larva), or: by the change in shape of the brain as a result of differential growth in certain regions of the brain (Weir, unpublished). The possible effect of synchronous growth in adjacent imaginal rudiments is unknown.

The measurement of imaginal buds as larval developmental markers.—Imaginal buds (of the wings and legs) have been utilised by Brian (1954) in the measurement of changes in the development of post-dormant larvae. Here measurement of the antennal bud gave more precise results during the early (precritical) instars. The early growth of this bud in larvae of *Myrmica* agrees with the observations of Tiegs (1922) on *Nasonia*. Stages in the structure and development of the antennal bud in *Myrmica* have been figured and described previously (Weir, 1959 c), where the critical developmental stage has been defined as the condition in which the length of the bud in optical section is 0.105 mm (35 units) and the length of the sheath in optical section is 0.015 mm (5 units).

EXPERIMENTS AND RESULTS

Growth and development of individual larvae.

In the course of experiments on larval growth which will not be described in detail but are similar to those described by Brian (1954), the measurement and observation of the growth of 180 individual larvae has produced the following conclusions.

1. Larvae enter dormancy in a condition where the brain may lie between 0.0 out of the head and 0.6 out of the head.
2. Measurement of the length of the antennal bud provides a more accurate measurement of the degree of pre-dormant development. Larvae may enter dormancy when the length of the antennal bud is between $22 + 3$ units and $35 + 5$ units (1 unit = 0.00295 mm), where 22 or 35 refers to the length of the bud, and 3 and 5 refer to the thickness of the basal portion of the sheath as seen in optical section.
3. Pre-dormant larvae (in which the brain becomes more than 0.6 out of the head, or in which the antennal bud is longer than $35 + 5$ units), can, if given suitable cultural conditions (optimal laboratory conditions), undergo metamorphosis within a short period of time (larval development via non-dormancy).

4. A correlation exists between larval size (total bulk) and the size of the antennal bud. The position of the brain being less easy to measure reliably shows greater variation relative to larval size.
5. The relationship of larval bulk to the growth of the antennal bud and brain position is different in pre-dormant as compared with non-dormant larvae.
6. In pre-dormant and dormant larvae there is a linear relationship between larval bulk and antennal bud measurements. In post-dormant or non-dormant larvae the relationship of growth of the antennal bud to increase in larval bulk shows a disproportionate size increase associated with the differentiation of the imaginal bud into the adult structure.
7. The start of this disproportionate growth of the antennal bud can be defined accurately in terms of the imaginal rudiments. It occurs when the brain is between 0.4 and 0.6 out of the head, and when the antennal bud and sheath are $35 + 5$ units in length, i.e. at the critical stage. Examination of the retrocerebral endocrine system at this time shows that "neurosecretory" material is detectable in quantity (for the first time in the third instar) in the corpus paracardiacum (Weir, 1959 c).
8. Experiments and observations on larval growth in several series starting with pre-dormant larvae of varying developmental conditions show that once a larva has passed this critical developmental stage, metamorphosis may follow rapidly, in optimal laboratory conditions. (Development via non-dormancy.)
9. It is difficult to avoid the conclusion that this critical developmental stage represents the earliest possible time of liberation in the third (the final) instar larva of a neurosecretory substance into the corpora paracardiacae. The time of liberation of this substance marks the onset of differentiation of the adult structures.
10. There is a range in size (and therefore development) of dormant larvae removed from the field. The causes of such a size range have been investigated both by the present author in experiments described below, and by Brian (1955 b). The effects of such a larval size (and development) range on the incidence of dormancy and the possible incidence of endocrinal diapause are considered.

The effect of worker seasonal condition.

Differences in the brood rearing potentiality of workers of three seasonal conditions* were investigated in experiment 1. Workers were of three

* The terms prevernal, vernal, aestival, and serotinal are defined by Brian (1954) and Weir (1958 a) and describe worker seasonal condition, referring to workers in the field in March, May, July and September respectively, or overwintered workers after 2 weeks, 5 weeks, 8 weeks, and 11 weeks culture at 25°C. respectively.

kinds—vernal overwintered workers, serotinal overwintered workers, and callow workers (produced three weeks previously from overwintered larvae). Six cultures were used, each containing 25 larvae, 25 worker-laid eggs, and 25 workers. Three of the larval groups were of large first instar larvae, three of early third instar larvae. Results after 7 days culture at 25°C. are shown in Figure 1. Three variations of larval develop-

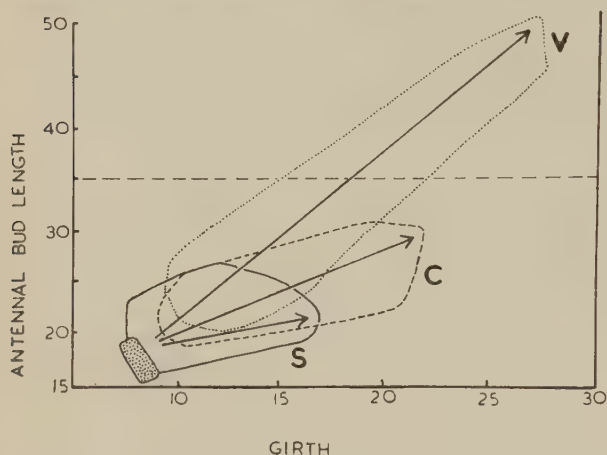


FIG. 1. — This shows diagrammatically the three developmental courses followed by larvae in experiment (1).

V = vernal workers; C = callow workers; S = serotinal workers.

The arrow indicates the maximal distance travelled along each course by larvae of the three groups, during seven days. All larvae start initially from the stippled region. The line round each arrow includes all the larvae in each group. The dotted line at antennal bud length 35 indicates that this is the critical developmental stage.

Units of girth—derived by calculation and are of purely relative significance.

Units of antennal length—1 unit = 0.00294 mms.

callos workers produced an intermediate group of larvae, and vernal workers produced the best growth and development. There was a range of larval growth and development in all cultures. Certain larvae in each culture showed little progress. The significance of this experiment lies in the differing course of development produced in those larvae which showed the greatest growth and development in each culture. It is apparent that different larval developmental courses are associated with workers of different seasonal conditions. Within seven days from the start of the experiment, certain third instar larvae (including some which were initially in the first instar) reached and passed the critical developmental stage described above, and therefore were determined for non-dormancy (Fig. 1).

Experiment 2 was designed to eliminate certain group effects, caused by preferential worker treatment of certain larvae, which obscured the importance of worker condition.

ment attributable to the three worker types are shown. Corresponding development occurred in first instar and third instar larvae. The arrow refers to the course of development of that larva in each group which developed furthest. The developmental courses of other larvae within each group all fall within the area bounded by the line enclosing the appropriate arrow.

Course divergence is shown clearly both by groups starting in the first instar and by groups starting in the third instar.

Serotinal workers showed least success,

Experiment 2 consisted of ten cultures each containing three early (pre-critical) third instar larvae, and ten workers. Workers were from two sources, either all vernal or all serotinal. No workers derived from brood of the current season were included. The average larval development in the two series of cultures after 14 days at 25°C. is shown in Figure 2. In this experiment the use of small larval groups largely overcame the problem of biased feeding and within each culture larvae showed similar growth and development. No larva cultured by serotinal workers reached the critical larval developmental stage. All except one of the larvae cultured by vernal workers reached and passed this critical stage.

It is apparent from this experiment that larvae in the early third instar may enter upon either of the developmental courses, i.e. development via non-dormancy or development after dormancy.

Differences in successive groups of larvae produced by one colony.

For experiment 3 a colony containing twenty workers and one queen of *M. rubra microgyna* in early aestival condition was collected and cultured at 25°C. Callow workers, pre-pupae, pupae and residual larvae derived from the overwintered brood were removed from the colony. Third instar larvae produced in this colony were examined at eight day intervals, and those which were seen to have passed the critical developmental stage when examined were removed and discarded. Results are shown in Figure 3 and in Table I.

The tabulated figures of wing bud area, limb bud area, and uric acid volume have been derived by calculation from the original data and no absolute values can be assigned to the units. At the first census, the onset of limb bud segmentation has prevented accurate measurement of the large areal increase and the numbers of segments (S) are indicated instead.

In successive groups of larvae reaching the critical stage, there was a steady increase in the area of residual food in the gut proportional to the total area of the larva. This was associated with a change in colour of

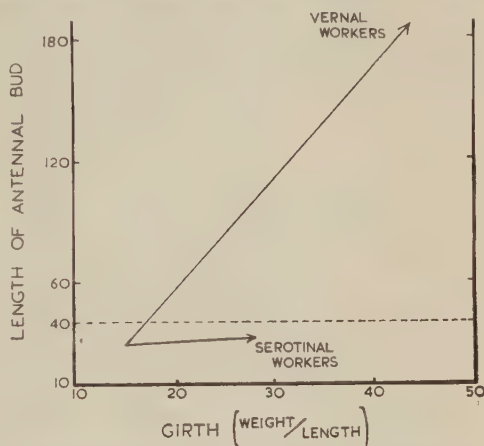


FIG. 2. — This shows the average course development of the 2 larval groups in experiment 2 after 14 days. Final data on all larvae within each group were averaged, and this data is indicated by the tip of the arrow. The initial data were also averaged. All data were closely similar. The dotted line represents the critical antennal bud + antennal sheath length of 35 ± 5 units (where 1 unit = 0.00294 mms.) and the girth is a calculated value derived from weight and length.

TABLE I. — THE INITIAL CONDITION OF LARVAE IN EXPERIMENT 3 COMPARED WITH LARVAE REMOVED DURING THE THREE SUCCEEDING CENSUSES.

		MEASUREMENTS UNDERTAKEN.				
		% brain outside head capsule.	Length of antennal bud.	Area of wing bud.	Area of limb bud.	Volume of malpighian tubule occupied by uric acid crystals.
INITIAL VALUES.	Max.	0.5	35+5	5	9	20
	Av.	0.3	32+4	4	8	10
	Min.	0.1	25+3	3	4	4
CENSUS 1.	Max.	1.0	150	15	4S	22
	Av.	1.0	145	10	3-4S	7
	Min.	1.0	120	6	3S	2
CENSUS 2.	Max.	0.4	35+5	6	9	27
	Av.	0.3	30+3	3	6	20
	Min.	0.2	23+2	2	3	6
CENSUS 3.	Max.	0.4	30+4	4	6	34
	Av.	0.2	25+5	3	4	26
	Min.	0.0	20+2	2	2	11

the residual material from pale yellow to dark brown. The amount of uric

acid accumulating in the malpighian tubules increased as did the bulk of the fat body while decreases in the rate of development as measured by the antennal bud length, the brain movement, wing buds and limbs are noted in Table I.

It seems that during the aestival condition there is a change in the quality and perhaps quantity of food in the larval gut. This might be due to a change in the trophic properties of aestival workers. This gradual change in larval food is contemporaneous with a gradual change in larval course development.

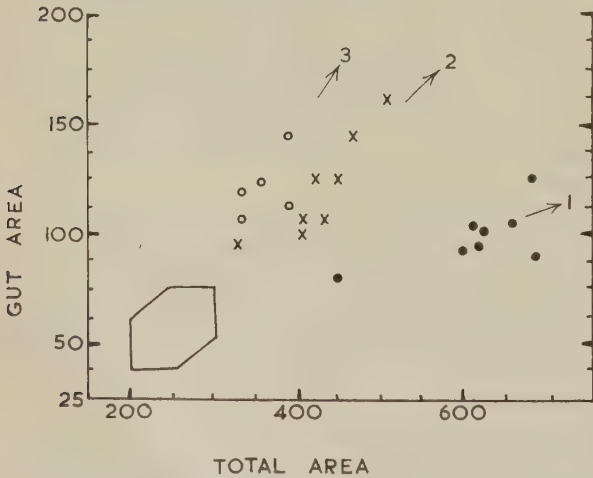


FIG. 3. — This shows the relationship of total larval area to gut area in the three groups of larvae removed at successive intervals of eight days in experiment 3. Group 1 (8 days) is denoted by dots, group 2 (16 days) by crosses and group 3 by circles. Arrows indicate the direction of larval progression from the initial polygonal area within which all early third instar larvae lay.

*Investigation of synthetic and unbalanced larval diets
and of the C/N ratio.*

In Experiment 4, three groups of ten aestival workers were pretreated for 14 days before the experiment was set up. One group was fed on a high protein diet (*Drosophila* larvae), one group on sucrose (low protein), and one group on both. Each of these three groups was then cultured with ten early third instar larvae while continuing to receive the same diet as it had previously received for 14 days. Differences in the larval gut and urine after this period were as follows:

- High protein — voluminous dark brown gut;
 - urine voluminous, cloudy, containing numerous white uric acid crystals;
 - malpighian tubules white, opaque, and full of uric acid crystals.
- Sugar only — moderate-sized gut, pale brown in colour;
 - small amount of urine, no uric acid crystals in urine;
 - malpighian tubules with very small numbers of uric acid crystals.
- Sugar and Protein — moderate-sized gut, pale brown in colour;
 - voluminous urine, a few crystals of uric acid;
 - malpighian tubules containing some uric acid crystals.

Thus appearances resembling those observed in Experiment 3 can be produced by alteration of the carbo-hydrate/nitrogen ratio of the food. Sugar, however, does not, in this case, produce the pale yellow colour observed in the gut of non-dormant larvae reared by vernal workers.

Analyses of total nitrogen content by the micro-kjeldahl method of Ma and Zuazaga (1942) have been made on larvae at certain developmental stages and after culture by certain seasonal worker types. The analyses described below were made on larvae from one colony of *M. rubra microgyna* throughout one season (Experiment 5). The colony was collected in vernal condition and analyses were made of non-dormant larvae, but in Figure 4 it is convenient to show these analyses as a continuous seasonal series (i.e., in the reverse order). In Figure 4, line A-B indicates the change from the critical stage to prepupation in non-dormant larvae, line C-D the equivalent change in medium-sized dormant larvae producing workers, and line D-E the equivalent change in large dormant larvae producing queens.

The ejection of a meconium at prepupation causes further complications. This meconium may be largely formed before the larva reaches the critical stage. Meconia vary in size and, therefore, presumably in nitrogen content.

These estimations of total nitrogen must include a high proportion of "structural" nitrogen in the cuticle and internal organs. A suggested value (probably an underestimate) has been inserted in Figure 4, and shows as a result that the percentage change in "non-structural" nitrogen content between dormant and non-dormant larval groups is probably

important. The amount of nitrogenous material ingested prior to the critical stage may control the course of larval development. It seems, therefore, since Figure 4 includes brood destined to become queens, that the ingestion of quantities of nitrogenous material by pre-dormant larvae may play some part in caste differentiation.

Artificial diets have been used to determine whether simple changes in the carbo hydrate/nitrogen (C/N) ratio can control larval course development from the first instar. None of these experiments has been successful with first instar larvae. The results of an experiment (6) using second instar larvae are shown in Table II. Each culture contained four

TABLE II. — THE AVERAGE LENGTH OF LARVAE (WHERE 1 UNIT = 0.0625 MM.) SURVIVING AFTER FOURTEEN DAYS IN TWO EXPERIMENTS USING A SERIES OF FIXED C/N RATIOS. (The number of larvae surviving in each culture is shown in brackets below the average larval length.)

	CULTURES.							
	1	2	3	4	5	6	7	8
CASEIN IN GMS. (Nitrogenous food).	—	.1	.5	2	2	2	2	2
SUGAR IN GMS. (Carbo-hydrate).	2	2	2	2	.5	.1	.01	—
EXPERIMENT I.	42 (3)	40 (4)	27 (3)	30 (1)	32 (2)	— (0)	— (0)	— (0)
EXPERIMENT II.	39 (4)	39 (3)	37 (1)	30 (2)	— (0)	32 (1)	21 (2)	— (0)

second instar larvae and ten pre-treated workers. Workers had been reared on a diet of an appropriate C/N ratio for ten days before the experiment.

The significance of these results is obscured by differences in larval mortality. These differences may be attributable to inefficiency on the part of the workers in certain cultures, lacking in sugar. Preliminary evidence from experiments using casein and other proteins, sugar, and oleic acid, in various proportions, shows that none of these were as successful for larval brood rearing as *Drosophila* larvae and sugar. Similar technical objections may affect experiments using vital dyes. However, results from these experiments appear to confirm that sucrose is fed to non-dormant larvae. The first incidence of worker feeding was detected in

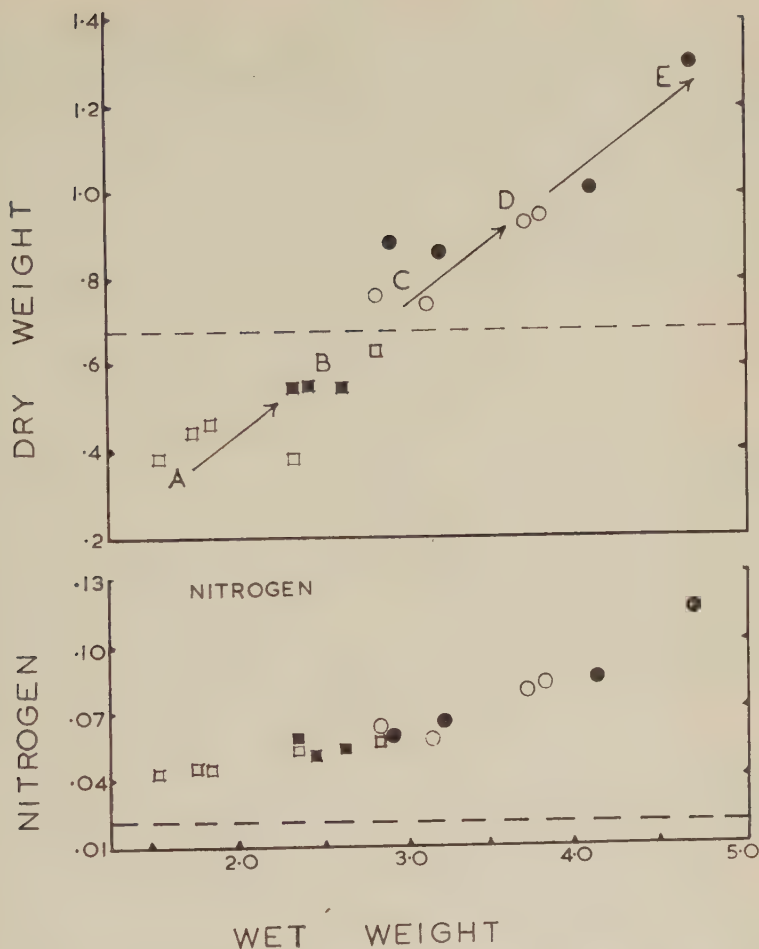


Fig. 4. — Shows the results of nitrogen analyses of 160 larvae in groups of 10. The regression of larval dry weight on larval wet weight is apparent. All weights are expressed in milligrams as the averaged value for one larva.

The dotted line in the upper portion indicates that line above which all larvae and pre-pupae are post-dormant (circles and dots), and below which all larvae and pupae are non-dormant or predormant (squares).

White circles and white squares indicate larvae. Black circles and black squares indicate pre-pupae.

The dotted line in the lower portion indicates a possible level of structural nitrogen, i.e. that of cuticle, head capsule, etc.

A = Non-dormant larvae.

B = { Non-dormant pre-pupae producing workers.
Predormant larvae.

C = { Post-dormant larvae.
Post-dormant pre-pupae producing workers.

D = { Post-dormant larvae producing queens.
Post-dormant pre-pupae (producing larger workers than in C?).

E = Post-dormant pre-pupae producing queens.

It should be recollected that the condition of prepupation is characterised by the ejection of the meconium. There is therefore an actual loss of total nitrogen at prepupation.

certain relatively large, late, first instar larvae. These showed traces of dyes associated with sucrose. It is unlikely, judging by intensity of colour and gut volume, that this diet consisted solely of sugar. [Various trophic relations between larvae and workers have been investigated in a number of genera by Le Masne (1953).] Le Masne describes a number of cases where larvae have been observed receiving food previously ingested by workers. It appears that here, non-dormant larvae were fed on a sugar rich diet which may be mixed with the salivary secretions of the larvae themselves, of certain of the workers, or with yolk from eggs. The diet of dormant larvae included large quantities of allochthonous protein.

Range in size of dormant larvae and possible occurrence of diapause.

The two main causes of the range in larval size at dormancy may be stated as follows:

- A. Biassed feeding of larval groups. Experiments previously described have shown that a size range of larvae is inevitably produced after the culture of an initially uniform group of larvae by a group of workers. The causes of such differential growth in laboratory nests may be attributable to possible laboratory artifacts such as brood piling (Weir, 1958 *b*, 1959 *b*; Brian, 1956). There is some doubt as to whether brood piling occurs in nature where differences in the growth of an initially uniform larval group may be due to other causes.
- B. Differences in the time of production of larvae in the field. It is known (Brian, 1951) that some dormant larvae may be produced from the first (vernal) egg peak. All larvae produced during the second (aestival) egg peak become dormant. Such a range in the time of production of larvae may provide a basis for differential growth and development in nature prior to dormancy (Weir, 1959 *b*).

Experiments with serotinal (hibernating) larvae have been undertaken to determine:

1. The ability of sub-critical (pre-dormant) larvae to grow and develop towards the critical stage.
2. The ability of critical pre-dormant and dormant larvae to undergo post-critical growth and development.

The growth of 35 sub-critical, serotinal, small, and medium-sized *M. rubra microgyna* larvae, each cultured in isolation with four workers of varying seasonal conditions, showed that all small larvae and certain medium-sized larvae could increase in girth, without becoming post-critical, i.e. could show growth without post-critical development. Certain small larvae could also become post-critical and undergo metamorphosis, if reared with vernal workers.

The growth of small and medium-sized larvae in groups of three also produced the same results. Further clarification of this problem is derived from an experiment carried out by Brian (1955 *b*). A short account of this experiment is given here:

Twelve cultures each containing 20 sub-critical larvae and 40 workers of *M. rubra macrogyna* were cultured, six at 20°C. and six at 25°C., larval size and worker condition also being varied throughout. The variation in the proportion of larvae to each size group undergoing metamorphosis varies both with the condition of the workers and with temperature. Considering, for example, only those cultures reared by vernal workers at 20°C.:

Large larvae :	4 metamorphosed, 16 remained dormant at the same size as at the start of the experiment.
Medium-sized larvae :	7 metamorphosed, 14 remained dormant with slight bulk increase.
Small larvae :	11 metamorphosed, 6 remained dormant.

Hese results show that the numbers of larvae metamorphosing in each size group also vary with worker quality (vernal as opposed to aestival, vernal workers causing a higher percentage metamorphosis) and temperature (25°C. as opposed to 20°C., 25°C. causing an increased percentage metamorphosis). The effect of group size in this experiment is obscure (Brian, 1956).

Therefore it appears that if a condition of physiological diapause (endocrinal diapause) comparable to those described by Lees (1955) exists in certain of these female larvae, then:

1. workers can break this diapause;
2. the rigidity of this diapause is not comparable to that seen in insects such as *Hyalophora* (*Platysamia*) *cecropia* (Williams, 1952), since it can be broken to varying extents by workers of different seasonal conditions working under differing environmental conditions.

If a true endocrinal diapause does occur, it may be that it is restricted to large and medium-sized larvae and then only to certain of these larvae. (Even under optimal laboratory conditions at 25°C. with vernal workers, metamorphosis was not achieved by all larvae of all size groups. Specifically, 66 % of large larvae, 50 % of medium-sized larvae metamorphosed.) The incidence of diapause might then be considered to vary with the bulk of the gut or of the fat body, or both (Andrewartha, 1952). Recent evidence suggests that laboratory conditions may not be optimal, since excessive food may be provided, by comparison with conditions in the field. Nest design is also important.

In a further experiment (7) the growth and development of 30 individual larvae was measured. Each larva was cultured with four vernal workers on a high protein diet (*Drosophila* larvae) for a period of 65 days. All workers had been pretreated for 14 days by feeding on *Drosophila* alone. Ten larvae were large, ten medium-sized and ten small. The results of this experiment are shown in Figure 5, as the average value of the resulting developmental courses, in a plot of the growth of the antennal bud against time.

Metamorphosis was confined to large larvae (4/10 metamorphosing rapidly). No other larval size groups showed prepupation even after 65 days. There was a large increase in bulk in all groups. This result is irreconcilable with the incidence of diapause solely in relation to the bulk of the fat body and/or the gut. All larvae showed development past the critical stage defined previously and ceased to develop at a subsequent stage, characterised as follows.

The brain lay between 0.7 and 0.9 in the prothorax. The antennal

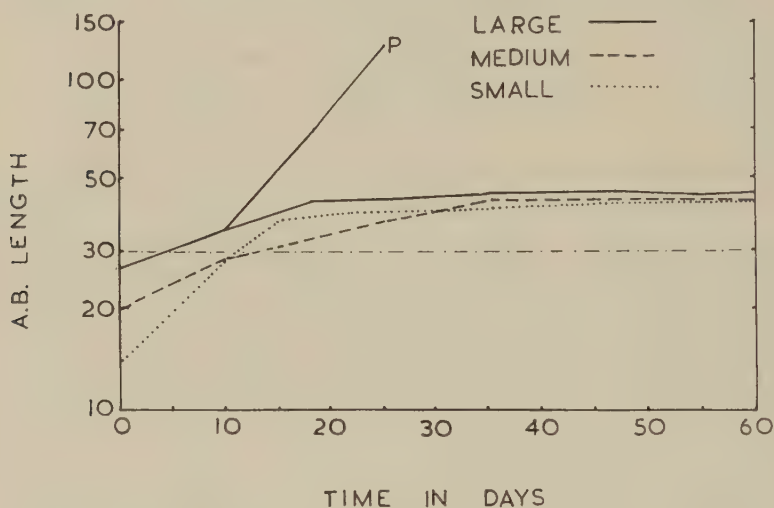


FIG. 5. — This shows the 4 averaged developmental courses exhibited by larvae in experiment 7. There was close agreement among individual larvae following all of these courses, so individual developmental courses are not shown. For convenience the 5 units of length have been deducted from the antennal bud length. The critical value now becomes 30 units and this is indicated by the dotted line.

L = Large larvae; M = Medium sized larvae; S = Small larvae. P = Prepupae.

bud length varied between 52 (bud) + 5 (sheath) and 65 (bud) + 20 (sheath) (where 1 unit = 0.00295 mm). The limb buds were either two segmented or were at an incipient three-segmented stage. It was difficult to measure accurately the area of the wing buds in view of the large bulk of fat body. This stage appears to be similar to that described by Brian (personal communication) in *Myrmica rubra macrogyna* where the limb bud is also two-segmented.

Nine larvae from Experiment 7 were sectioned. The corpora paracardica were distended and showed traces of chromophil material, from which it appeared that neurosecretory material had been released.

A decrease in gut area following the starvation of all cultures for one week (after 40 days) showed that although there was throughout a constant ratio of total area to gut area in all larvae, the larvae are being fed continuously but are unable to show increases in growth or development.

Following this period of starvation all larvae were hand-fed with sugar solution. No increased growth or development resulted within one week. The following week sugar was added to all cultures, and all larvae become prepupae within seven days.

DISCUSSION AND CONCLUSIONS

Definitions are given for convenience of the usage in this discussion of certain physiological terms.

Diapause. — Refers to larvae shown to be unable to take advantage of optimal experimental conditions for growth and development, a condition whose control can be related to the retrocerebral endocrine system (Lees, 1955).

Environmental Restriction. — Refers to larvae which are unable to grow and develop because of adverse environmental conditions. It may be noted that in *Myrmica*, worker condition and worker behaviour type are aspects of the larval environment.

Dormancy. — Refers to larvae which are overwintering in the field, or which are not growing and developing (in the laboratory). This term therefore includes both diapause and environmental restriction.

Non-dormancy. — Refers to larvae which are developing into adults within the same season in which they hatched.

Differences in the seasonal condition (physiological state) of workers control the growth and development of larvae towards non-dormancy or dormancy (Experiment 1). Vernal workers produce non-dormant brood. In nature, the production of non-dormant larvae is associated with late vernal and early aestival workers. Vernal workers are associated in nature with the production of gyne larvae from the post-dormant (vernalised) brood. (Brian, 1954, 1955 *a*, 1955 *b*, 1956 *a*.) Serotinal workers produce dormant larvae. These workers are present in colonies in the field when dormant larvae are produced and are mixed with callow workers from the two brood batches. It may be concluded that larval development towards dormancy or non-dormancy can be regulated by serotinal workers alone.

The result of Experiment 1 is obscured by biased feeding of certain larvae in the group. Such effects are circumvented in Experiment 2. It can be concluded that the size and initial composition of the larval group (Weir, 1959 *b*) affects, in Experiment 1, the number of larvae which are determined for dormancy or non-dormancy, and the rate at which these larvae are determined.

Callow workers have a positive effect, intermediate between that of vernal workers and serotinal workers. It appears that they may produce non-dormant brood, but take a longer time to do so than vernal workers. If they are present and functional in a natural, vernal colony they will

therefore exert a delaying effect on the rate of production of the non-dormant brood.

Since early third instar larvae are as developmentally plastic as first instar larvae (Experiment 1), the determination of larvae for dormancy or non-dormancy must take place, at the earliest, shortly after the start of the third instar. However the larvae may be directed towards one or other of these developmental paths by random factors operating perhaps even in the egg mass, and certainly immediately following the disruption of the egg mass. (Weir, 1959 *b*). Experimentally these effects can be reversed in the third instar.

Successive broods reared by aestival workers show a series of changes. (Experiment 3.) The changes from the production of non-dormant to dormant brood tended by aestival workers is gradual and is accompanied by changes of gut content, fat body, malpighian tubule content, etc., which are similar to those produced by a range of synthetic diets (Experiment 6), or controlled diets (Experiment 4), in which the sugar/protein ratio is varied. It is concluded that there is a gradual change in the diet fed to the larvae by aestival workers.

Chemical analyses of a series of larvae and pupae throughout the year show that there is an increase in the ratio of nitrogen to carbon. Dormant larvae contain significantly greater quantities of nitrogen both in the meconium and in the fat body (Experiment 5).

Previous work has shown that there is, in all colonies examined, a range of worker behaviour from workers which "prefer" to forage to workers which "prefer" to nurse. (Weir, 1958 *a, b*). This polyethal system has been shown to be dynamic. Such a polyethal system implies that the protein flux of the colony at any one time may be a function of the number of workers which "prefer" to forage or which are displaced from nursing or other activities by a shift of equilibrium, such as the production of a new batch of workers with strong "preferences" for nursing. Yet it has been shown that "pure cultures" of such workers do not control the determination of larvae for dormancy or non-dormancy (Weir, 1958 *b*). Factors such as worker locomotor activity, behaviour, size, melanisation, killing potential, or oviposition potential are not limiting factors with regard to the induction or non-induction of dormancy, in the laboratory. It therefore appears that the changes of worker seasonal condition may be physiological and involve qualitative changes in glandular activity, changes in nitrogen composition being only a concomitant effect. Seasonal trophic variation in adult *Polistes* is described by Deleurance (1950, 1955) where qualitative differences of glandular secretions, temperature differences, and possibly quantitative effects also cause a change in larval food which leads to the death of the colony in the autumn. While worker locomotor activity, behaviour, size, melanisation, killing potential, and oviposition do not limit the induction or non-induction of larval dormancy in laboratory conditions, it is possible that these factors could be limiting in conditions of food shortage, such as may frequently exist in nature.

Two further points will be considered. First, the possible incidence of diapause, and second, the significance of callow workers.

Weir (1959 *c*) has investigated the retrocerebral endocrine complex in larvae of *Myrmica* and its relationship to the larval brain. Results show that the condition of the developmental markers in the living larva can be related to changes in the retrocerebral endocrine complex. The "critical stage" of determination for dormancy or non-dormancy is, in fact, the first time when "neurosecretory" material may appear in the corpora paracardiacia (if the larva is going to become non-dormant) and so lead to the induction of metamorphosis. In dormant larvae, development ceases at this critical stage but growth may continue without the appearance of "neurosecretory" material in the corpora paracardiacia. From this it may seem that a condition of diapause could be postulated. Yet other work (Brian, 1955 *b*) has shown that diapause, if it occurred, must occur only in certain larvae, the percentage occurrence varying with larval size. Investigation of a series of larvae of varying sizes has failed to reveal any qualitative differences in the retrocerebral complex between the larvae (Weir, 1959 *c*). Any pronouncement of the incidence of larval diapause therefore rests on experimental analyses, since transplantation experiments were unsuccessful.

No conclusive evidence of diapause in serotinal larvae has been obtained here. Experiments have shown that under controlled conditions of low temperature and restricted food, growth and development can be halted, apparently indefinitely. (Experiment 7). This is a case of environmental restriction, not diapause, since readjustment of the environmental conditions is followed rapidly by pupation. It should also be noted that, in Experiment 7, the readjustment appeared to be effective via the workers. The concept of a worker diapause, with concomitant effects on larvae, has numerous possibilities.

Among the possible causes of larval diapause which have been investigated are egg size variation due either to temperature variation or to differences of intra-colonial origin (Weir, 1958 *c*), as described by Flanders (1953) in *Cryptus* and *Spalangia*, and temperature variation (Weir, 1958 *c*, 1959 *b*, and above experiments). Causes of diapause induction following temperature variation have been reviewed by Andrewartha (1952) and Lees (1955). If these factors have any influence on the induction of diapause in *Myrmica*, the effects are obscured by differences of larval mortality under experimental conditions.

A true diapause could occur during the summer, as a form of aestivation. This has not been investigated.

The callow workers (Experiment 1) have a positive delaying action in brood development by comparison with vernal workers. In the field large numbers of callows appear in nests in the early summer within a short period of time. They appear a few days after the start of eclosion in the large egg mass accumulated by the queen in conjunction with vernal workers (Brian, 1951; Weir, 1958 *c*, 1959 *b*). The possible effects of such

a batch of callow workers "arriving" in a theoretical colony at this time is visualised as follows:

The conditions necessary for the accumulation of the egg mass have been described by Weir (1959 *a*, 1959 *b*). When these become favourable accumulation is rapid, and results in a large batch of eggs of which approximately half may survive to become larvae. These may have a range in age of about 2 to 10 days at 25°C. In the egg mass, the first larvae to hatch are directed towards non-dormant development (Weir, 1959 *b*). Late vernal workers tend these larvae and determination for non-dormancy results. About this time, the batch of callows appears. Callows show strong pro-larval preferences, so nurses tend to be displaced from the brood mass with resultant dilution of nurse effort. The rate of production of non-dormant brood slows down. The positive effect of the callows (Experiment 1) reinforces this slowdown. Thus the older workers have ceased to be vernal and are in aestival condition when the next larvae approach the critical determination stage. These larvae will be determined for dormancy. This delay will operate in proportion to the number of callows produced from the first brood hatch. It might be considered that this sequence of events implied social inefficiency. This is not the case.

If worker brood rearing of overwintered larvae produced a large quantity of new workers (callows), these stop the production of more workers (via non-dormancy) in proportion to their numbers, and divert the pre-critical larvae towards dormancy, i.e., towards potential queen path development. If, on the other hand, few workers were produced in the spring, the small number of callows will not significantly interfere with the determination of larvae for non-dormancy and the rapid production of more workers during the summer. Worker effort is directed towards the most useful ends at the latest point in time where control can be exercised. In other terms, the effect of dilution of vernal worker effort by the sudden appearance of a batch of callows can be seen as a form of negative feed back in one part of an oscillatory circuit. This circuit is capable of producing either workers or queen potential larvae and thereby relating previous worker achievement to future larval potentiality. This influx of workers tends also to synchronise this oscillator with other oscillators in the circuit, e.g., the worker mechanism controlling sudden egg accumulation [as opposed to other possible effects (Weir, 1957 *a*) where in certain cases, oviposition is gradual, and resultant larvae would show a wide range in size and age]. The separate systems of colonial sociology can be seen as a series of oscillators, all capable of free-running in isolation (Weir, 1959 *a*). When oscillations are initiated, normally by the environment for *Myrmica*, throughout the complete circuit, positive feed back is only possible at one frequency or at harmonics of that frequency. Thus the oscillators become suitably synchronised, even in the absence of any immediate environmental timer. This may be compared with the "reverberatory" system described by Schneirla (1957) for *Eciton* and similar

also to that of *Anomma*, (Raignier, and van Boven, 1955), where the alternation of statary and nomadic phases is not synchronised by the environment. Oscillation has been established at a much higher frequency in *Eciton*. This model is unsatisfactory since the experimental evidence described here and elsewhere shows that social integration tends to cause the sudden switching on and off of the individual components. This causes the abrupt rise and rapid fall in output of the several components, giving an output effect to be compared with a "square wave" more than a "sine wave". In electronic terms, a better model for the overall activity pattern of *Eciton* might be the free-running multivibrator (square wave generator). In this the action of one half of the circuit (e.g., the statary phase) produces a certain constant and recognisable output, while, at the same time, it causes a sequential series of changes of state in the circuit the effect of which is to switch itself off after a fixed period of time, and cause the abrupt operation of the other half of the circuit (e.g., the nomadic phase). This in turn switches itself off after a fixed period of time and brings the other (statary) phase into abrupt operation. The duration of operation of each phase is determined by the components in the circuit, and the process can continue indefinitely. In *Myrmica*, environmental triggering suggest a triggered multivibrator (or flip-flop) as a more accurate model. The same principle is utilised but the circuit does not normally free-run. One portion of the circuit (e.g., egg production) is triggered by environmental factors, and this eventually brings the second half of the circuit into operation as before. In reality, any comprehensive model would have a number of flip-flops, synchronised both among themselves and to the environmental trigger.

In *Myrmica* periodicity imposed by the seasonal environment is adapted by the colonial sociology (via individual ontogenetic plasticity) to allow maximal sociological flexibility counteracting the enforced physiological periodicity. Plasticity of larval development via non-dormancy or dormancy is not, in this case, the ecophysiological adaptation of the individuals of the species to an unfavourable environment (as it often is in insects) but the socio-physiological adaptation of the colony to facilitate colony survival and colony reproduction.

Zusammenfassung.

1. Es ist durch Experimente gezeigt worden, dass Ruhe und Nichtruhe bei *Myrmica* von der Nahrungszufuhr abhängig sind und dass sie deswegen durch die Arbeiter bestimmt werden.
2. Larven werden für Ruhe oder Nichtruhe früh im dritten Abhäutungsstadium bestimmt.
3. Der physiologische Zustand der Arbeiter wechselt mit der Jahreszeit, indem Frühlingsarbeiter nichtruhende Larven, die Herbstarbeiter

ruhende Larven entwickeln, während die Sommerarbeiter zuerst nicht-ruhende, danach ruhende Larven entwickeln.

4. Die unreifen Arbeiter üben einen hemmenden Einfluss auf den Wuchs und die Entwicklung der Larven aus.
5. Die Grösse der Eimasse und der sich daraus ergebenden Brutmasse ist von Wichtigkeit; denn sie beeinflusst die übermässige Nahrungseinnahme gewisser Larven, die infolgedessen in den Stand der Nihtruhe gesteuert werden.
6. Der Stickstoffinhalt der Nahrung nimmt im Laufe des Jahres zu; Nahrungsunterschiede können durch künstliche Diäten mit wechselndem Verhältnis zwischen Zucker und Eiweiss nachgeahmt werden.
7. Frühere Experimente lassen vermuten, dass Unterschiede im Strom des Eiweisses im Laboratorium nicht kritisch sind.
8. Die Möglichkeit, dass qualitative Unterschiede in der Drüsensekretion bei den Arbeitern von kritischer Wichtigkeit sein könnten, wird besprochen.
9. Es ist möglich, den Zeitpunkt der Bestimmung der Larven für die Ruhe oder die Nihtruhe in der individuellen Entwicklung mit dem Zeitpunkt, in welchem die Neurosekretion in dem dritten Abhautungsstadium in den *corpora paracardiac*a zuerst ermittelt werden, in Zusammenhang zu bringen. Dieses Stadium in der Larvenentwicklung kann durch Anlagen genau festgestellt und erkannt werden.
10. Die Möglichkeit des Zuvorkommens einer zwangsmässigen Ruhe bei den Larven wird besprochen. Diese Experimente heben keine überführenden Beweise dafür geliefert, obwohl Stockungen in Wuchs und Entwicklung experimentell herbeigeführt werden können.

Summary.

1. Experiments show that larval dormancy and non-dormancy in *Myrmica* are trophogenic and controlled by the workers.
2. Larvae are determined for dormancy or non-dormancy in the early third instar.
3. The nitrogen content of the diet increases during the year and trophic differences can be simulated by artificial diets with varying sugar/protein (fat-body) ratios.
4. There is evidence to suggest that variation in the flux of crude protein and fat (*Drosophila* larvae) as opposed to sugar is not critical, under laboratory conditions.
5. Worker physiological condition changes throughout the season, vernal workers producing non-dormant larvae, serotinal workers producing dormant larvae, and aestival workers producing first, non-dormant and then dormant larvae.
6. Callow workers have a delaying action on larval growth and development.

7. The size of the egg mass and of the resultant brood mass is of importance since this affects the biased feeding of certain larvae which are so directed towards non-dormancy.
8. It is possible to relate the time of determination for dormancy or non-dormancy in individual ontogeny to the time at which the paracardiac secretion is first detected in bulk during the third instar. This stage of larval development can be accurately defined and recognised by developmental markers.
9. The possible occurrence and importance of glandular secretions produced by workers is considered. The possible incidence of larval diapause is also discussed.
10. The significance of sudden influxes of batches of callow workers is discussed. It is shown that this will increase social efficiency.
11. A model is described in electronic terms which compares periodicity in *Myrmica* with that in *Eciton*. The significance of sudden changes of state is emphasised.

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COLONY DEVELOPMENT IN *CUBITERMES* *UGANDENSIS* FULLER (ISOPTERA : TERMITIDAE)

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This paper concerns the development of incipient colonies after the establishment of dealate pairs in the soil. Studies of flight and colony foundation in this species and in *Cubitermes testaceus* have been described in a previous paper (WILLIAMS, 1959). This work formed part of a general study of the two species made between February 1955 and January 1956, first at Kawanda Research Station, near Kampala, Uganda, and then from November 1955 at the East African Agriculture and Forestry Research Organisation, Kikuyu, Kenya Colony.

Material and methods.

Cubitermes ugandensis is a grassland species, wide-spread in Uganda and occurring also in adjacent parts of most neighbouring territories. The material used for this work was taken from grassland swamp-border areas near Kawanda. The distribution of this termite and the source of material have been described in greater detail in the previous paper mentioned above, in which methods used for the flying of alates in the laboratory and the establishment of dealate pairs in soil filled glass plates have likewise been described.

Plates were kept flat in darkened chambers which maintained relative humidity at or approaching 100 %, except during rapid rises of temperature for which there was no control. Laboratory temperatures at Kawanda were found to range most commonly from about 20-21°C in the early morning to about 26-27°C in the afternoon. At Kikuyu the altitude is greater and conditions much cooler. There, the laboratory was heated to give a range of temperature close to that usual at Kawanda.

RESULTS AND DISCUSSION

A.—The Imagos.

Feeding. — *Cubitermes ugandensis* is a soil feeding termite. The imago pairs therefore establish themselves within their food, unlike the subterranean wood feeders of the Termitidae which apparently subsist on their own food reserves until they have produced foraging workers.

Imagos were frequently observed feeding on the soil. Faecal soil was used by the pair to line the glass floor and roof of the cell. When the cover glasses of the plates were lifted off for cleaning, this faecal soil was always

replaced within a few days. Larvae wounded during ecdysis were eaten, as would be expected, and others also on occasions, probably in most cases following accidental wounding during grooming. Very rarely, an egg was seen in the early stages of decay, but such eggs were always eaten when they became flaccid. On the other hand the surviving imago of a pair would seldom eat any part of a dead partner, though occasionally some parts of the extremities might be very slightly mutilated. This was probably due to the modifications of behaviour which resulted almost immediately from the survivor being left on its own. Imagos of either sex installed on their own, or left on their own by the death of a partner, would become sluggish, perform scarcely any building or burrowing work, would feed only desultorily, producing little faeces, and would die within a few days or weeks. Groups of imagos however would eat the whole or part of a dead imago and bury any uneaten part.

Antennal Mutilation. — The eating of parts of the extremities, particularly the antennae, of each member of the pair by its partner has been noted by a number of authors concerned with various groups. It appears to occur generally within a few days of pairing and entry into the nest. During these observations on *Cubitermes ugandensis* no note was made of the earliest day on which such mutilation took place. By the 68th day after pairing the imagos of the 26 surviving male-female pairs were seen all to have lost 1-5 segments of each antenna, there being no obvious difference between the sexes in the number of segments lost. The remaining 5 females of two female groups, each originally of 3 females, had all lost a similar number of segments by the same day. 6 pairs of males had all lost 1-2 segments of each antenna by the 16th day after installation.

Grassé (1942) considered that there was no obvious practical reason for antennal mutilation and that in fact a practical reason might not exist. It is evident from the above data that there is no connection between antennal mutilation and sexual behaviour. The need for extra food can scarcely arise when the pair have installed themselves in the food on which a large colony may be raised. Moreover, the amount of material involved, so far as the female is concerned, is minute, scarcely enough for the production of a single egg. There is no necessity for antennal mutilation in *Cubitermes testaceus*, although it does take place as is evident from collected specimens. 11 pairs of this species, all subsequently successful in producing larvae, had not lost any segments of their antennae after nearly two months.

Antennal mutilation should probably be regarded as an example of ordinary cannibalism. As a rule, cannibalism among termites involves only dead, sluggish or wounded individuals. A cannibalistic attack is not always fatal, the severity of the attack depending on the activity of the victim, for the attacker or attackers do not approach in a hostile manner and can easily be evaded by an active victim. Other mutilations may take place in some cases. The male of one *C. ugandensis* pair lost a leg in this

way within 5 days of foundation. *Zootermopsis* imago pairs kept by the author in London, under conditions resulting in successful colony development, have in a few cases shown mutilation of mouthparts and legs besides those of the antennae. Buchli (1950 *b*) has described how grooming among imago pairs of *Reticulitermes lucifugus*, may lead to mutilations and thence sometimes to fatal cannibalism. Buchli mentions mutilation of legs in particular in this case, but antennal mutilation is apparently usual in this species (Grassé, 1942). It seems reasonable to class all such mutilations together, but they appear at first not readily comparable with the ordinary cannibalism of termite colonies, since they take place between fit and unwounded individuals. However, the constriction of the cell in the early days after foundation, and the consequent inactivity of the imagos, may make each imago appear sluggish to its partner, thereby stimulating cannibalistic attacks by each on the other. Other contributing factors, such as the physiological state of the imagos at this time, may of course be present also. So long as the imagos are active in evading such attacks, the comparatively vulnerable antennae are the first parts likely to suffer.

First Copulation. — It was necessary to find out by experiment at what time after entry into the soil copulation might take place, since continuous observation was not possible. An experiment was therefore devised in which the males of pairs were removed after various intervals.

70 tandem pairs, flown in the laboratory, were each allowed to burrow into the soil at the edge of a glass plate. The plates were grouped into 7 series, each of 10. Then the males were removed from all but one of the series after different intervals. Thus series were obtained in which the females had been with males for 0.5, 1, 2, 3, 4 and 5 days after entry into the soil, together with a control series of ordinary pairs. Each tandem pair was carefully checked for sex before being allowed to enter a plate and, after entering the plate, was left in the dark as undisturbed as possible until the male was removed.

A test had already suggested that females could not be expected to live long or to behave normally on their own, whereas pairs or groups of females could be expected to maintain the activity and general behaviour of those of heterosexual pairs, as in *Reticulitermes lucifugus* (Buchli, 1950 *a*). This was further born out by the course of the experiment, in which companion virgin females were used. The use of workers as companions was rejected, despite the fact that they would be readily replaceable if unfit, because their likely reaction to lone females and brood was uncertain. Buchli found that single virgin females placed with a few workers were neglected, behaved abnormally and did not live long.

Accordingly, a large number of females were removed from the flight chamber during the flights for the production of tandem pairs, dealated artificially and marked each with a small spot of quick drying paint on the dorsal abdomen. They were kept temporarily in large groups in soil filled plates and, later, one added to each plate from which a male was removed.

The distinguishing of the companions from the experimental females by marking should have allowed the replacement of any companion that became unfit. This could be done without affecting the experiment, and was desirable since casualties among the companions could be expected, due to the excessive handling they received compared with the experimental females. A pool of companions was maintained for this purpose but unfortunately was destroyed by fungus disease. The losses that occurred were, in consequence, greater than would otherwise have been the case, all except one being due to the death of the companion, causing the early decease of the experimental female.

The surviving plates were examined about ten days after the first appearance of larvae among them. Those with developing eggs present and/or larvae were classed as fertilised. The remainder which had only eggs showing no signs of development were classed as unfertilised. The results are given in Table 1.

TABLE 1.

EXPOSURE TO MALES. DAYS.	FEMALES FERTILISED.	FEMALES UNFERTILISED.	FEMALES DIED.
0.5	0	10	0
1	0	10	0
2	0	8	2
3	4	5	1
4	3	5	2
5	6	3	1
Indefinite (Control)	10	0	0

Although the series proved too few for determination of the maximum likely time elapsing between entry into the soil and copulation, the results indicate that copulation is unlikely before the third day under these conditions. The period of two days after entry into the soil corresponds with the approximate period necessary for completion of the cell by heterosexual pairs under similar conditions (Williams, op. cit.).

Failure after copulation in either fertilisation of eggs or in egg laying would introduce error in interpretation of the results. However, in addition to the wholly successful control series of 10 pairs, 26 out of 29 other male-female pairs kept under similar conditions were successful in producing fertilised brood, the 3 failures being due to premature death of the imagos. One may conclude, therefore, that error due to abnormalities other than those leading to early death of the imagos would be negligible. Parthenogenesis would also cause error and has been found to occur readily in *Zootermopsis* spp. (Light, 1944) and very occasionally in *Reticulitermes hesperus* (Weesner, 1956). In *C. ugandensis* it clearly does not occur readily as otherwise few plates, if any, would have lacked developing

eggs and/or larvae. The occurrence of an occasional parthenogenetic egg in this experiment is unlikely as the fertilised and unfertilised groups were so clearly separated on the basis of brood number, due, mainly at least, to the mortality of unfertilised eggs. At the close of the experiment the number of eggs in the 'unfertilised' plates ranged from 2-8, mean c.4.5. The number of eggs and larvae in the 'fertilised' plates, excluding the control series, ranged from 11-19, mean c.14.5. Such a clear separation would not have been found had the 'fertilised' group included plates in which the brood was, in fact, unfertilised, but in which one or two eggs had developed parthenogenetically. Moreover the minimum number of clearly developing eggs and larvae in any of the 'fertilised' plates was 6. It is improbable that as many eggs as this would develop parthenogenetically in one plate unless parthenogenesis occurred readily, as it clearly does not.

Care of Brood. Both sexes appeared to take a more or less equal part in assisting at the hatching of eggs and moulting of larvae. The attraction of exuviae seemed to be intense, of much the same degree as the attraction of a dead or wounded individual, and in fact such assistance would readily turn to cannibalism if the larva or callow worker was accidentally wounded during the moult. Immature workers were sometimes attracted to moulting individuals.

The males appeared to take the greater part in the feeding and grooming of larvae, as noticed in the case of *Reticulitermes lucifugus* by Buchli (1950 b). The larvae of both instars were fed on stomodeal food and no traces of soil in the gut were ever seen. On one occasion a worker was seen to receive stomodeal food on the second day after ecdysis when the gut still contained a little air. The characteristic flattening of the abdomen of immature workers at a later stage suggests that they receive very little of this food, if any, once the integument has hardened.

B.—The Brood.

29 male-female pairs were obtained from laboratory flights on 20.vi.55 for the study of brood production. 26 pairs produced larvae and in 24 cases these developed into workers. Failures were due to the death of the imagos in 4 cases, while the 5th was due to heavy and continued mortality of larvae. Most pairs were allowed to burrow into the soil at the edge of a glass plate, but some were placed each in the centre of the plate in a ready made chamber, from which they each carved off a cell without burrowing. Egg laying nevertheless began on the 5th day after foundation among some pairs in both groups, and no subsequent differences between the groups was noted.

Brood Production. — Figure 1 shows the course, to the 149th day after foundation, of a colony the development of which was near average for the 24 which produced workers. No precise information on brood mortality was obtained. Rates of brood production were gained only from the periodical counts of brood and are therefore the effective rates, likely to be slightly lower than the true rates. The total of brood began to fall in some colonies after the 114th day after foundation and in all colonies after the 149th day. This fall was characterised particularly by high worker mortality. It appeared clearly due to deterioration as food of the soil in

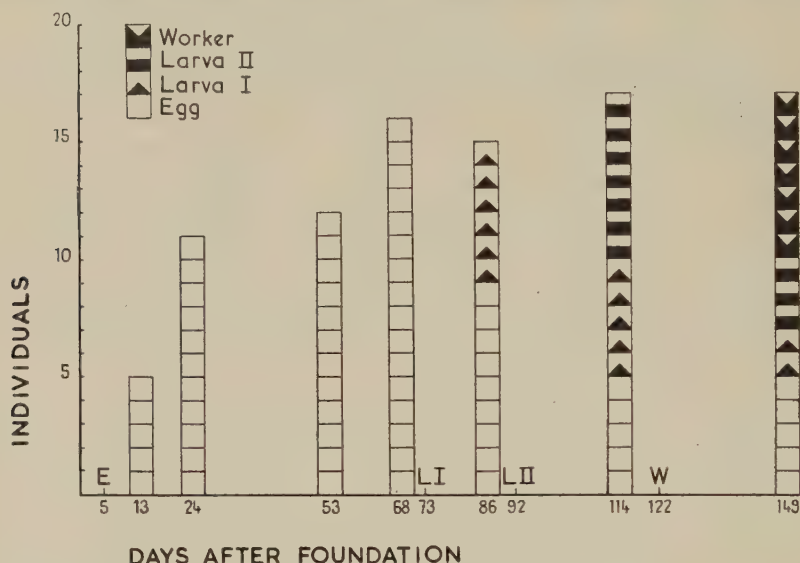


FIG. 1. — Brood production in a typical laboratory colony. Letters indicate the appearance of the first individual of each developmental stage.

the plates, since quantities of excretory products appeared in the fat bodies of the workers, progress through the soil was unduly slow, and the soil when compared at a late stage with fresher soil from the same source was found to have become greyer and more crumbly. This soil deterioration factor may have been effective long before the workers were produced and may have influenced egg laying rates at an early stage. However, eggs were still being laid at a slow rate 206 days after foundation when the imagos were in a very unhealthy condition, so the effect of this factor on the laying rates during the first two months or so is not likely to have been very great. It is unlikely to have greatly affected the early pattern of brood production, or the development of larvae, which appeared to maintain their usual activity to the 206th day, in contrast to the imagos and workers. On the other hand, brood counts after production of the first worker are not considered of value.

All colonies produced eggs at a rapid rate between the 5th and 13th day

after foundation, averaging 1 egg/c.1½ days, the majority continuing at a similar rate in the 13-24 day period. The rate then fell sharply between the 24th and 53rd day in most colonies, between the 13th and 24th in a few. This fall off was followed by a resurgence at a rate lower than the initial one, averaging 1 egg/c.5½ days, rather lower than the mean rate up to the period of resurgence of 1 egg/c.4½ days. Between the 68th and 86th days, during which period larvae were produced, most colonies showed a second fall off, the brood count in many cases remaining steady or falling. This was due at least partly to hatching mortality, and was followed by a further resurgence when the larvae from the initial fast laying period had all been hatched. The maximum number of workers noted in any colony was 12, on the 185th day after foundation at which time the mean number per colony was 7. No soldiers were produced by any colony. It is unlikely that a soldier nymph was produced at any time as none was seen in spite of frequent brief examinations of the colonies.

Brood Development. — The data of Table 2 concern 23 colonies which produced workers. In one further colony, the appearance of the first worker was considerably delayed by larval mortality and the data for that colony are omitted.

TABLE 2.—THE CHRONOLOGY OF BROOD DEVELOPMENT.

EVENT.	DAY.
—	—
Foundation	0
1st. Egg	5-c.12
1st. Larva I	72-76
1st. Larva II	92-99
1st. Worker	119-128

The duration of each developmental stage was taken as the number of days elapsing between the appearance in each colony of the first individual of the stage concerned and that of the next. The mean periods so obtained are likely to be slightly longer than the true means due to mortality among such first individuals. The incubation period of eggs was obtained accurately from only 5 colonies, in which the range was 67-69 days. Data for the duration of the two larval stadia are given in figure 2, the mean values being 21.9 days for stadium I and 28.5 days for stadium II.

These developmental periods, particularly that of the egg, are longer than might be expected by comparison with those recorded for various other termites by the authors cited in this paper, notably those concerned with Termitidae, including Grassé & Noirot (1955). Light & Weesner (1955), and also Lüscher (1951) whose studies included *Cubitermes glebae*. At one *Cubitermes* locality temperatures of the ground, near the surface beneath grass cover, were taken on a few occasions and were found to approximate reasonably to laboratory temperatures at appropriate times

of day. However, it is uncertain whether or not this was generally the case, and moreover the temperature ranges at the depths to which pairs burrow, presumably at least several cm., would be narrower than that at the surface, with a higher minimum temperature.

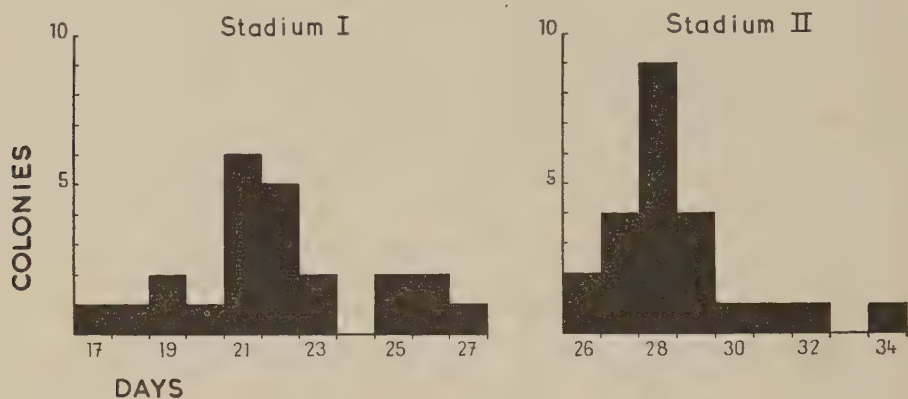


FIG. 2. — The duration of larval stadia, obtained as described in the text.

The Worker Immaturity Period. — The worker immaturity period is taken as that elapsing between the completion of the last ecdysis and the filling of the gut with soil. Softness and paleness of the integument appeared, rather indefinitely, to be corrected by the 2nd or 3rd day when the worker was nearly always still inactive and immature in behaviour. The course of events in a quickly maturing worker would be as follows:

- Day 0 Integument transparent, abdomen cylindrical, much air in gut. Inactive.
- Day 1 Firmer creamy integument, abdomen less cylindrical, little air in gut.
- Day 2 Integument firm, abdomen flat, traces of soil in gut but no air. A little more active.
- Day 3 Appreciable amount of soil in gut but abdomen still nearly flat. More active.
- Day 4 Abdomen fully or almost fully filled out with soil. Associating actively with other mature workers.

This period is of interest in that it offers a possible method of calculating life length under natural conditions. Limits, I_1 and I_2 , can be calculated for the true mean immaturity period with $C\%$ confidence. Similar confidence limits, P_1 and P_2 , can also be calculated for the true proportion, expressed as a fraction, of immature workers in a sampled worker population. The proportion of immature workers in a population represents an equivalent proportion of the mean life length of the population. This proportion is equal to the mean immaturity period, provided that there

is no mortality during that period. Neglecting this last obvious error, the limits of mean life length, L_1 and L_2 , are found by the following formula:

$$L_1 = \frac{I_1}{P_1} \quad \text{and} \quad L_2 = \frac{I_2}{P_2}$$

with $\frac{C^2}{100}$ % confidence. The following example is calculated only to reasonable approximation, as it is subject to errors, including that mentioned above, which are discussed below.

The immaturity periods of 66 workers, observed among the incipient colonies, is shown in figure 3. The mean value is 5.6 days, with standard error 0.2. It may be said with 99 % confidence that the true mean lies within the limits 5.1-6.1 days. A large active *C. ugandensis* colony was sampled at Kawanda. This sample, taken at points all through the mound, included 6,581 workers, of which 133 were immature, i.e., 0.022 of the sample. The 99 % confidence limits for the true proportion of immature workers in that colony are 0.018 and 0.026. In accordance with the above formula, then, the mean worker life length lies within the limits 196 and 339 days with 98.01 % confidence.

This particular result may be subject to at least the following errors, considering only those which might be reduced by further investigation. The proportion of immature workers in the mound at the time of sampling may not have been close to the average yearly proportion due to seasonal variation in brood production. This is unlikely to be a serious error as the climate at Kawanda varies comparatively little throughout the year, while imago brood, when in production, must form only a small fraction of the whole. Secondly, the maturation period in a large colony may differ from that in a small incipient colony. In the latter the immature workers are always in comparatively close contact with fresh soil, and may therefore mature on average more quickly. Thirdly, the proportion of immature workers in the mound is almost certain to be greater than that in the colony as a whole because, until the integument has hardened, they are very inactive and unlikely to leave the mound. Lastly, there must be some mortality during the maturation period; this would have the effect of raising the calculated limits and would tend to offset the lowering of the calculated limits by the second and third errors. This last error is not likely to be very great as only 2 of 68 workers studied failed to complete the maturation period. The second and third errors, the third almost

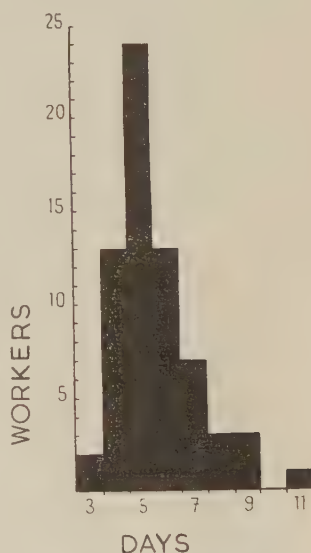


FIG. 3. — The duration of the immaturity period in 66 workers of incipient colonies.

certainly present, may be considerable. The above estimate is therefore probably a conservative one.

C.—Colony Survival.

The imagos of 2 colonies died by the 5th day after foundation and those of a 3rd colony by the 13th day, the cause of these losses being unknown. 1 colony was lost between the 86th and 114th days following the accidental killing of the female. 3 further colonies were lost between the 149th and 206th days, these losses being almost certainly due to the soil deterioration mentioned above.

The common natural causes of loss after foundation were clearly either removed by the laboratory conditions or did not appear. Among probable minor causes of post-foundation losses, are accidents such as crushing in soft ground by large animals. Starvation, which probably accounts for many pairs of wood-feeding Termitidae, would be unlikely to cause much loss in the case of this soil feeding species; the extensive collection from East Africa made by the Unit indicates that many *Cubitermes* species, including *ugandensis*, will live on a wide variety of soils, distribution appearing to depend mainly on other factors. Dehydration might cause loss in some areas within the distribution of *C. ugandensis*, but is unlikely at Kawanda and similar areas in eastern Uganda near Lake Victoria, where some rain is to be expected even in the 'dry' season.

Flooding, on the other hand, is likely in swamp border areas. However, as flight follows heavy rain, the water table is likely to be fairly high at the time of colony foundation, barring the choice by pairs of the more readily flooded parts. Mounds occur only on parts of the swamp borders which are seldom, if ever, completely inundated. They are, however, found on parts where the water rises almost to ground level after very heavy rain, suggesting that pairs and incipient colonies must be able to withstand occasional immersion. Flooding immediately after foundation might well be fatal, for, although workers can survive several hours under water and imagos may well have a similar ability, the walls of the burrow would be likely to collapse on the pair. Once the cell has been constructed and lined with faeces the danger would be greatly reduced, as the walls would be less likely to collapse and the cell would, moreover, retain trapped air.

Loss is to be expected by disease. This was not excluded by laboratory conditions although no disease was seen among these colonies. In the course of various experiments, losses among *C. ugandensis* workers were caused by a disease characterised by the presence in the hind gut of numerous uniflagellate protozoa. Whether or not a defence against this disease exists in large colonies is unknown. It was never noticed in large laboratory colonies, but its course in groups of up to 15 workers suggested that those of a small incipient colony would be readily killed by it. A rapidly fatal and highly infective fungus of the Entomophthoraceae,

attacking imagos, workers and soldiers at least, occurred in this species. The same or a similar disease was seen more frequently in *C. testaceus*. It was found that laboratory colonies of *C. testaceus* with a worker population of about a thousand or more could defend themselves successfully against this disease in a way that will be described in a further paper. Incipient colonies of this species including fewer than several scores of workers would probably not survive if an individual died of this disease in the nest. The defence was noted in both *C. ugandensis* and *C. orthognathus* and although no close study of the disease was made in these species the above remarks almost certainly apply equally to them.

Predation by ants other than Dorylines may take place after foundation. There is some evidence, however, to be published in a further paper, that those ants of the Camponotinae and Myrmicinae most commonly found in *Cubitermes* mounds at Kawanda will not take *Cubitermes* workers as prey and are inclined to avoid them under undisturbed conditions, although they will attack them if the mound is broken up in the field. Doryline ants, on the other hand, probably cause considerable losses after colony foundation. At Kawanda the subterranean *Dorylus* (*Anomma*) *kohli* Wasmann (1) was not infrequently met with when soil was turned over in the *Cubitermes* localities. On two occasions this ant was found attacking large mounds, one of *C. ugandensis* and the other of *C. testaceus*. These colonies survived although the attack on that of *ugandensis* persisted for some three days. It was found by partial dissection of the mounds that the ants may penetrate at least 10 cm into the heavily populated parts of the mound at some points, apparently becoming increasingly hindered by the confusion of dead termites and cell walls. A colony not consisting of many thousands of individuals, in a mound less than 20 cm wide, would be unlikely to survive such an attack.

The fungus disease would constitute a major danger to the colony for at least a year or two after foundation, and *D. kohli* probably for several years. The disease of the gut was not studied sufficiently for such a judgement to be made. Studies at Kawanda revealed no factors likely to cause greater loss of young colonies than these.

Summary.

Imago pairs of *Cubitermes ugandensis* Fuller, maintained in the laboratory, fed readily on soil, on the exuviae of brood, on dead and occasionally on living brood. Antennal mutilation occurred in both homo- and heterosexual pairs, and appeared comparable with ordinary cannibalism. It was found by experiment that copulation was unlikely before the third day after foundation in the conditions of the laboratory, this period

(1) Kindly identified by Dr. I. H. H. YARROW of the *British Museum* (Natural History).

corresponding with that necessary for completion of the cell. In the course of this experiment, it became apparent that parthenogenesis is rare, or absent, in this species. Both sexes assisted equally at the hatching of eggs and moulting of larvae, but the males were the more active in the feeding and grooming of larvae.

Egg laying commenced some pairs on the 5th day after foundation. The characteristic pattern of egg production included an initial period of fast laying for c.2-3 weeks at a rate of 1 egg/c. $1\frac{1}{2}$ days; this was followed by a period of c.4 weeks during which few eggs were produced, and then by a resurgence of laying at a rate of 1 egg/c. $5\frac{1}{2}$ days. The chronology of brood development is given and discussed. No soldiers were produced in any colony although as many as 12, and an average of 7 workers were present among the colonies at one time. The immaturity period of young workers is noted, and is considered a possible means of estimating worker life length under natural conditions.

The survival of colonies is noted. Two diseases and predation by *Dorylus (A.) kohli* are discussed as probable major causes of failure of young colonies under natural conditions.

Résumé.

Les couples d'imagos de *Cubitermes ugandensis* Fuller, gardés dans le laboratoire, se sont nourris assez volontiers d'humus, des exuvies de couvains, de faux couvains et parfois de couvains vivants. Des mutilations d'antennes se sont produites parmi les couples tant homo- que hétérosexués et semblaient comparables au cannibalisme ordinaire. Des expériences ont démontré que la copulation est peu probable avant le troisième jour suivant la fondation de la colonie dans le laboratoire, cette période correspondant, du reste, à celle requise pour l'achèvement de la cellule. Au cours de cette expérience, il est apparu que, chez cette espèce, la parthénogénèse est rare, sinon absente. Les deux sexes s'entraidaient également dans le travail d'éclosion et de mue des larves, mais les mâles s'avéraient plus actifs quant à l'alimentation et au léchage des larves.

Pour certains couples, la ponte commença dès le cinquième jour après la fondation. La courbe caractéristique de la ponte comprenait une période de ponte active d'environ deux à trois semaines, au taux d'un œuf par un jour et demi environ; cette période était suivie, *primo*: d'une autre d'environ quatre semaines, au cours de laquelle peu d'œufs étaient pondus; *secundo*: d'une recrudescence de la ponte au taux d'un œuf par cinq jours et demi environ. On donne la chronologie du développement des couvains. Aucun soldat n'a été produit dans aucune colonie, malgré la présence dans les colonies, à un moment donné, d'ouvriers au nombre de douze, et en moyenne de sept ouvriers. L'auteur décrit la période d'immaturité des jeunes ouvriers et la considère comme offrant la possibilité d'estimer la durée de vie des ouvriers dans des conditions naturelles.

On donne les détails de la survie des colonies. On discute deux maladies et les déprédations de *Dorylus (A.) kohli* comme causes majeures probables de l'échec de jeunes colonies dans des conditions naturelles.

Zusammenfassung.

Im Laboratorium gezüchtete Imagopaare von *Cubitermes ugandensis* Fuller ernährten sich bereitwillig von Erde, Larvencuticula, sowie toten und gelegentlich auch lebenden Eier und Larven. Antennenverstümmelung kam sowohl bei gleich- als bei ungleichgeschlechtigen Paaren vor und ist anscheinend mit gewöhnlichem Kannibalismus vergleichbar. Den angestellten Versuchen zufolge erscheint Kopulation vor dem 3. Tag nach der Koloniegründung als unwahrscheinlich, und dieser Zeitraum ist übrigens der für die Herstellung der Nestkammer erforderliche. Der Verlauf dieser Versuche scheint anzudeuten, dass Parthenogenese bei dieser Art selten oder überhaupt nicht vorkommt. Beide Geschlechter befassten sich in gleichem Ausmasse mit der Ausbrütung und Häutung der Larven, wobei jedoch die Männchen sich bei die Fütterung und Pflege der Larven als eifriger erwiesen.

Bei manchen Paaren begann das Eierlegen am 5. Tag nach der Gründung. Der charakteristische Verlauf der Legezeit umfasst eine Anfangsperiode von etwa 2-3 Wochen raschen Eierlegens, u. zw. 1 Ei etwa alle $1\frac{1}{2}$ Tage; während der nächsten etwa 4 Wochen wurden nur wenige Eier gelegt, und dann erfolgte eine Beschleunigung des Eierlegens auf 1 Ei etwa alle $5\frac{1}{2}$ Tage. Der Verfasser beschreibt die chronologische Brutentwicklung. Keine Kolonie hat Soldaten hervorgebracht, obwohl sich zu gleicher Zeit bis zu 12 und im Durchschnitt 7 Arbeiter in den Kolonien befanden. Der Verfasser beschreibt die Unreifezeit junger Arbeiter und ist der Ansicht, dass sie evtl. als Massstab für die Abschätzung der Lebensdauer der Arbeiter unter natürlichen Lebensbedingungen dienen könnte.

Der Verfasser bespricht das Ueberleben von Kolonien. Er schildert zwei Krankheiten und Raub seitens *Dorylus (A.) kohli* als wahrscheinliche Hauptursachen warum junge Kolonien unter natürlichen Lebensbedingungen zugrundegehen.

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